REGENERATION OF COMMERCIAL TREE SPECIES FOLLOWING CONTROLLED
BURNS IN A TROPICAL DRY FOREST IN EASTERN BOLIVIA

by

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Dedicated to my parents,

Margaret Kennard and Robert Kennard,

and to my husband,

Josh McDaniel

TABLE OF CONTENTS

5 EFFECTS OF CANOPY GAP FORMATION, PLANT REMOVAL, AND CONTROLLED
    BURNS OF HIGH AND LOW INTENSITIES ON A DRY FOREST PLANT
    COMMUNITY

6 COMMERCIAL TREE SPECIES REGENERATION FOLLOWING AGRICULTURAL
    ABANDONMENT IN BOLIVIAN DRY FORESTS

7 SUMMARY AND CONCLUSIONS

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Low levels of disturbance associated with selective logging may be insufficient for the
establishment of many Bolivian dry forest timber species, the majority of which are shade-
intolerant. To examine the ecological potential of prescribed burning as a silvicultural tool, I
compared the effects of canopy opening, plant removal, and controlled burns of high and low
intensities on 1) soil properties; 2) establishment, growth, and survival of commercial tree species;
3) and, plant community structure and composition. To describe commercial tree regeneration over
longer time scales, I characterized tree population structures in abandoned slash-and-burn fields
ranging in age from 1-50 years, and compared these to a mature forest stand.

Both high- and low-intensity burns caused a dramatic but temporary increase in soil
nutrients. High-intensity burns altered several soil physical properties, whereas low-intensity burns
had little effect. Plant removal and canopy opening had little effect on soil chemical and physical
properties.

Three responses to gap treatments were observed among commercial tree species. 1) Shade-intolerant species regenerating from seed were most successful following high-intensity burns. 2) Shade-tolerant species were most abundant in treatments where survival of their advanced regeneration was most likely (gap control and plant removal). Some of these species had the ability to survive controlled burns by sprouting. 3) Individuals of root sprouting species were most abundant following plant removal and low-intensity burns.

Sprouts dominated regeneration following canopy opening, plant removal, and low-intensity burns. In contrast, seedlings dominated following high-intensity burns. High-intensity burns shifted species composition relative to the less disturbed treatments.

Regeneration of shade-intolerant timber species was most abundant in young slash-and-burn fallows. Similar tree population structures in older slash-and-burn fallows and the mature forest stand suggests that the mature forest likely formed following a large-scale disturbance.

Although prescribed burning enhanced the regeneration of shade-intolerant timber species, it is not likely to become a forest management tool in Bolivia in the near future due to economic and political factors. Managing secondary forests in Bolivia would provide an alternative to current attempts to regenerate these species after selective harvesting of mature forest.

CHAPTER 1
INTRODUCTION

Introduction

Eastern Bolivia contains some of the largest and most diverse tracts of tropical dry forest in Latin America. Natural forest management for timber, if profitable, is one means of discouraging conversion of these forests to competing land uses. However, insufficient regeneration of many commercial timber species presently poses an ecological barrier to sustained timber yield, prompting forest managers to explore additional silvicultural methods to enhance regeneration of these species. The low levels of disturbance associated with highly selective logging may be insufficient for the establishment of many dry forest timber species, the majority of which are shade-intolerant and likely require moderately intense disturbances for their establishment. Fire, of both natural and anthropogenic origins, has likely been a pervasive influence on tropical dry forests, and therefore, prescribed burning may be an effective silvicultural tool to enhance regeneration of timber species following selective logging.

In this dissertation, I present the results of studies that examined commercial tree regeneration following disturbances of various intensities in a dry forest in lowland Bolivia, including harvesting gap formation, controlled burns of high and low intensity, and slash-and-burn agriculture. My goal in carrying out these studies was to determine the regeneration requirements of these commercial tree species, as well as to examine the effects of potential silvicultural treatments on forest soils and community structure and composition.

Conservation and Management of Tropical Dry Forests

Tropical dry forests comprise approximately 42% of tropical forest land, more than either moist or wet tropical forests (Murphy and Lugo 1986). Tropical dry forests also have supported higher human population densities than wetter tropical forests for centuries (Murphy and Lugo 1986) and, as a result, have suffered more degradation and deforestation (Mooney *et al.* 1995, Murphy and Lugo 1995). Efforts to slow conversion rates of dry tropical forest have been negligible (Mooney *et al.* 1995). For example, in 1988, less than 2% of the original dry forest on the Pacific coast of Central America remained intact and less than 0.1% had conservation status (Janzen 1988). Consequently, tropical dry forests are considered by some ecologists as the most threatened of the major tropical forest types (Janzen 1988).

Given the extensive use of tropical dry forests by rural people, their strict preservation may not be a realistic conservation goal. As Johnson and Carbarle (1993) note, most developing tropical countries rarely have the luxury of opting for forest preservation over forest exploitation. Consequently, in most tropical countries, conversion of forested land continues to increase while the establishment of protected areas remains low (FAO 1999). Consensus is emerging among ecologists that protected areas, due to their small number and size, cannot effectively conserve the majority of tropical species (Hansen *et al.* 1991, Heinrich 1995, Bawa and Seidler 1998). Mounting concern over global declines of biodiversity has prompted many ecologists to look outside of parks and nature preserves to semi-natural areas that may help maintain, or at least slow the loss of, biodiversity (Sayer and Wegge 1992, Chazdon 1998).

Natural forest management, the sustainable production of timber from natural forest areas, has been proposed as a means of maintaining forest value, thereby deterring land owners from clearing forested land for other more profitable and destructive land uses (Poore *et al* 1989, Johnson and Carbarle 1993, Maser 1994, but see Rice *et al.* 1997). Although definitions of natural forest management vary, they usually encompass two ideas: first, a sustained yield of forest

products, and second, achieving this sustained yield through means that maintain other environmental services, such as biodiversity, soil quality, and hydrology (reviewed by Johnson and Carbarle 1993). By maintaining forests in a semi-natural state, natural forest management is viewed by some as a critical means of maintaining biodiversity (Hansen *et al.* 1991, Sayer and Wegge 1992, Frumhoff 1995, Heinrich 1995, Dickinson *et al.* 1996, Putz *et al.* in press, but see Bawa and Siedler 1998), particularly in regions where forests are in danger of conversion. And, despite the fact that few modern examples of economically viable natural forest management projects exist (e.g., Panayotou and Ashton 1992, Johnson and Carbarle 1993, Rice *et al.* 1997, Bawa and Siedler 1998, Bowles *et al.* 1998, but see Leslie 1987), the promotion of sustainable forest management has become a mainstay in international strategies for the protection of tropical forests (Bawa and Siedler 1998, Haworth and Cousell 1999). As Haworth and Cousell (1999: 62) explain "this approach has often been justified on the grounds that it is the result of a difficult choice between accepting, on the one hand, the inevitability of continued commercial logging of natural forests, which will cause some damage to the ecosystem, or, on the other hand, facing the complete loss of the forest to other causes."

Management of Tropical Dry Forests in Eastern Bolivia

The Chiquitania region in eastern Bolivia contains one of the largest and most diverse tropical dry forests in the neotropics (Gentry 1993, Killeen *et al.* 1998). Although there is currently 150,000 to 200,000 km^2 of relatively intact forest in Chiquitania, Dinerstein *et al.* (1995) identified this area as one of the most endangered ecosystems in the neotropics. Deforestation in the alluvial soils near the city of Santa Cruz is in excess of 80,000 ha year^{-1} (Killeen *et al.* 1998). This conservation threat comes largely from large-scale industrial agriculture, but other economic activities, such as cattle ranching, contribute to this rapid conversion of forested land. These trends mimic past events in Argentina, Paraguay, and Eastern Brazil where similar dry forests have been deforested and fragmented over the past two decades (Killeen *et al.* 1998).

Due to recent forest policy changes in Bolivia, natural forest management may now be a practical means of controlling deforestation in Chiquitania. In 1996, a new forestry law was passed that requires, among other features, management plans for all Bolivian forests (Nittler and Nash 1999). Bolivian logging companies now operate with management plans on an estimated 5.7 million hectares of forest and a total of 660,000 hectares of Bolivian forest has been certified as sustainably managed (Nittler and Nash 1999).

The Lomerio Community Forest, located in the center of Chiquitania, was the first Bolivian forest to be certified. Its 60,800 hectares are owned and managed by 27 communities of the Chiquitano indigenous people. The Chiquitanos have been managing their forests for 19 timber species, 5 of which are classified as highly valuable (Table 1-1). Acquiring and maintaining adequate regeneration of commercial tree species, a challenge faced by all natural forest managers, is particularly apparent in Lomerio. For example, seedlings and saplings of 12 of the 19 commercial species are rare in forest understories (Table 1-1). A lack of seed sources due to previous over-harvesting may account for the scarcity of regeneration among highly valued timber species. However, poor regeneration plagues most of the tree species that have only recently been harvested (Fredricksen 1999). Apparently, the current harvesting and silvicultural techniques employed in Lomerio do not create conditions appropriate for the regeneration of these species. A better understanding of the regeneration requirements of these commercial tree species is critical, as continued regeneration failures will undoubtedly compromise the long-term sustainable management of these forests.

The Role of Historic Disturbance Regimes in Forest Management

It is often assumed that forest management is more compatible with long-term sustainability if timber harvesting and silvicultural techniques are designed to mimic historic disturbance regimes (e.g., Pickett and White 1985, Oliver and Larson 1996, Attiwill 1994a, 1994b). Although this assumption has rarely been tested, ecologists argue that replacing harvested

Table 1-1. Table modified from Pinard *et al.* 1999 that reports characteristics of 19 commercial tree species of the dry forests of Lomerio. Species were matched to a general silvicultural system (even- or uneven-aged) based on their regeneration requirements. Timber value is based on market value in 1999.

		Timber value	Managment system	Adult rarity	Sapling rarity	Shade tolerance
1	*Amburana cearensis*	high	even	3	3	1
2	*Anadenanthera colubrina*	low	even	1	2	1
3	*Aspidosperma cylindrocarpon*	low	uneven	2	3	2
4	*Aspidosperma rigidum*	low	uneven	1	2	2
5	*Astronium urundueva*	low	even	2	3	1
6	*Caesalpinia pluviosa*	low	uneven	1	2	2
7	*Cariniana estrellensis*	low	uneven	2	2	3
8	*Cedrela fissilis*	high	even	3	3	1
9	*Centrolobium microchaete*	high	even	1	3	1
10	*Copaifera chodatiana*	low	uneven	2	3	3
11	*Cordia alliodora*	high	even	3	2	1
12	*Hymenea courbaril*	low	even	3	3	1
13	*Machaerium scleroxylon*	high	uneven	1	2	3
14	*Phyllostylon rhamnoides*	low	uneven	2	2	3
15	*Platymiscium ulei*	low	even	3	3	1
16	*Schinopsis brasilensis*	low	even	2	3	1
17	*Spondias mombin*	low	even	2	3	1
18	*Tabebuia impetiginosa*	low	even	1	3	1
19	*Tabebuia serratifolia*	low	even	3	3	1

Shade tolerance: 1 = high light only, large gaps; 2 = partial shade, small gaps;

3 = partial or full shade, understory.

Adult rarity (> 20 cm dbh): 1 common (> 5 ha^{-1}); 2 = intermediate (1-5 ha^{-1}); 3 = rare (< 1 ha^{-1}).

Sapling rarity (5-10 cm dbh): 1 common (>20 ha^{-1}); 2 = intermediate (5-20 ha^{-1}); 3 = rare (<5 ha^{-1}).

Even: even-aged managment system with group selection.

Uneven: uneven-aged managment system with single-tree selection.

trees without irreversibly damaging the residual forest is more likely to occur under conditions similar to those that formed the original stand (Uhl *et al.* 1990). The selective cutting systems used in many tropical forests are often justified on models of gap-phase regeneration in unharvested forests (e.g., Whitmore 1989, Hartshorn 1989, Gomez-Pompa and Burley 1991).

Gap-phase regeneration, however, is not the most appropriate model for tropical dry forests. Evidence suggests that single tree-fall gaps are smaller and less frequent in tropical dry forests than in moist or wet forests (Dickinson 1998). Rather, very large gaps caused by catastrophic disturbances more likely govern dry forest dynamics. In Central America for example, mahogany (*Swietenia macrophylla*) has been noted to regenerate in even-aged stands after hurricanes and fires (Lamb 1966, Snook 1996). The low level of disturbance created during highly selective logging appears to be a poor replicate of this disturbance regime, and possibly for this reason, natural regeneration of mahogany is scarce in most selectively logged areas (Verissimo *et al.* 1995, Gullison *et al.* 1996, Whitman *et al.* 1997).

In contrast to Central America, the agents of large scale disturbance have not been a topic of frequent study in Bolivian dry forests (but see Pinard and Huffman 1997). As hurricanes are absent in this landlocked country, it is likely that forest fires (both natural and anthropogenic) have likely been the most pervasive influence on Bolivian forests. Natural fires have historically influenced vast areas of Amazonian forest (Clark and Uhl 1987), particularly in dry or deciduous forests where dry fuels may favor lightning fires (Middleton *et al.* 1997). In fact, most radiometric dates of charcoal found throughout the Amazon correspond with the expansion of dry forests during the dry glacial epochs (Saldariagga *et al.* 1986, Goldammer 1993, Prado and Gibbs 1993).

As is typical in most areas of the tropics, humans likely have been the most common agents of forest fires in Bolivia. Although most tropical fires are set intentionally by humans for the purposes of forest conversion, traditional slash-and-burn agriculture, or grazing land management, many of these intentionally set fires escape (Uhl and Buschbacher 1985, Sarre and

Goldhammer 1996, Holdsworth and Uhl 1997, Cochrane *et al.* 1999). Consequently, human-caused fires presently contribute more to tropical fire regimes than natural fires (Fearnside 1990, Goldammer 1993, Cochrane and Schultze 1998, Nepstad *et al.* 1998, 1999, Goldammer 1999). And, it is likely this was true historically as well, as human population densities in South America have recovered only in this century to densities present before Europeans arrived (Denevan 1976).

Recent evidence from Bolivia reveals the susceptibility of seasonally dry forests to escaped human-ignited fires. Over 1 million hectares of Bolivian dry forests burned during a severe dry season in 1994 (Pinard *et al.* 1999), and over 3 million hectares burned in one month in 1999 (T. Fredericksen, personal communication). Evidence also suggests that dry forests are damaged less by wildfire than moister forest types (Mostacedo *et al.* 1999), which may also be indicative of the pervasive role fire has played in the formation of these dry forests.

The Potential of Prescribed Burning in the Management of Bolivian Dry Forests

Although most guidelines for natural forest management focus on ways of reducing damage to residual stands (Heinrich 1995, Pinard and Putz 1996, Haworth 1999), low-impact selective logging may not be a sustainable management strategy in dry forests because of the low levels of disturbance associated with this harvesting technique. In Lomerio for example, roads and skid trails covered only 2-4% of logged sites and felling gaps were generally only 40-70 $m^2 ha^{-1}$ after harvesting operations (Camacho 1996). Likely, this damage does not create sufficient canopy opening for the regeneration of commercial tree species, 12 of 19 of which were classified as having shade intolerant regeneration (Table 1-1).

Due to the pervasive influence fire has likely had on the formation and maintenance of seasonally dry forests in Bolivia, prescribed burns are a promising silvicultural tool for managed dry forests. Prescribed burns produce several effects that will likely increase regeneration of shade-intolerant tree species, including vegetation removal, mineral soil exposure, and nutrient release (Hungerford *et al.* 1990, Bond and van Wilgen 1996). The use of prescribed burning in

tropical forest management is not a new idea. Ground fires were used as early as the mid-1800s to enhance teak (*Tectona grandis*) regeneration in deciduous forests of South-east Asia (Dawkins and Philip 1998). Tropical forest managers have recognized the benefits of prescribed burns for several shade-intolerant timber species in addition to teak, such as sal (*Shorea robusta*) and several pine species (*Pinus;* Goldammer 1994, Rodriquez 1996).

In South America however, the use of prescribed burning to enhance tree regeneration in broad-leaf forests is rarely practiced. If fire is addressed in forest management policies, it is primarily in the context of fire prevention or exclusion from protected areas (e.g., Reis 1996, New Forestry Law *in* BOLFOR 1997). Particularly in Bolivia, the techniques of prescribed burning are not well developed and the effects of prescribed burns on dry forest structure and function are not well known.

Scope of Dissertation

The overall objective of this dissertation is to examine the ecological potential of prescribed burning for the management of seasonally dry forests in eastern Bolivia. To be a viable management strategy for the certified forests of Lomerio, prescribed burns must enhance regeneration of commercial tree species without causing irreversible damage to the residual forest. The negative effects of prescribed burns are likely to increase with increasing fire intensity (reviewed in Chapter 2). Therefore, in this dissertation, I compare the effects of harvesting gap formation, and controlled burns of high and low intensities on commercial tree regeneration, forest soils, and plant diversity.

The dissertation contains seven chapters. In the second chapter, I briefly review the effects of fire intensity on plants and soils, introduce the study forest, and describe four treatments that form the basis of Chapters 3, 4, and 5. The treatments represent the following four disturbance intensities: harvesting gap formation, above-ground biomass removal, and, controlled burns of low and high intensity.

In the third chapter, I examine changes in soil physical and chemical properties following the four treatments. I address the mechanisms underlying these changes by examining experimentally the separate effects of heat and ash on soil properties. I also discuss how each of these treatments, through their effects on soil properties, may influence tree seedling growth.

Commercial tree establishment, growth, and survival in each of the four treatments is evaluated in Chapter 4. As species' responses to disturbance often vary among regeneration guilds, I discuss the effects of each treatment by illustrating how they affect each guild differently. I relate these results to the different management strategies that are appropriate for different species groups.

The effects of silvicultural treatments are primarily aimed at enhancing regeneration of commercial tree species. Yet the impacts of these treatments on the remaining plant community are also of concern, particularly in Lomerio where the local indigenous population depends on the forest for a variety of other uses. In Chapter 5, I examine the response of the plant community to the four treatments, focusing on changes in the dominance of species, life forms, and regeneration modes (seedlings or sprouts) among treatments. I discuss these patterns in relation to their importance for commercial tree regeneration.

The studies presented in Chapters 2 though 5 represent patterns of regeneration over an 18 month period following the treatments. In the sixth chapter, I examine patterns of regeneration following burns over longer time scales using a chronosequence of secondary forests. I characterize tree population structures, stand structure, and species richness in abandoned slash-and-burn fields of 12 different ages, ranging from 1 to 50 years. Comparing these secondary forests to a nearby mature forest stand, I discuss the possibility that the dominance of shade-intolerant trees in this region may be the legacy of slash-and-burn agriculture.

In the final chapter, I summarize the chapters and discuss the ecological potential of prescribed burns for the management of Lomerio forests. I discuss how prescribed burning might

fit into the current idea of natural forest management in the tropics. I also raise several questions of the economical and political constraints to implementing controlled burns on a management scale in Bolivia.

CHAPTER 2
STUDY SITE AND TREATMENT DESCRIPTIONS

Introduction

Forest disturbances vary widely in their type, intensity, frequency, and scale (Pickett and White 1985). Despite this variation, disturbances, by definition, hold their most important character in common: they reduce the dominance of a site by established individuals and create openings for colonization and growth by new individuals (Canham and Marks 1985). As such, disturbances are the primary catalyst of forest stand dynamics (Oliver and Larson 1996).

After most forest disturbances, there is a temporary increase the availability of light, water, and nutrients. There are at least two mechanisms by which forest disturbance may increase the availability of these resources. The first is the reduction in rates of uptake or use of resources due to the loss of plant biomass. This effect is most apparent in the enhancement of light levels in canopy openings (Chazdon and Fletcher 1984) and increased soil moisture in gaps (Vitousek and Denslow 1987). Disturbances may also increase resource availability indirectly by altering rates and pathways of nutrient cycling. For example, increased soil moisture and temperatures following large-scale windthrow may temporarily increase nutrient availability by increasing the rate of decomposition of soil organic matter (Bormann and Likens 1979).

Fire is an increasingly common disturbance in tropical forests (e.g., Goldammer 1993, Bond and van Wilgen 1996, Fearnside 1990, Sarre and Goldammer 1996). A feature of fire that may set it apart from other disturbances is its effect below-ground. Fire acts as a rapid decomposer, returning some nutrients from above-ground biomass to soil more rapidly than other disturbances (e.g., Humphreys and Craig 1981, Hungerford et al. 1990, Neary et al. 1999). The

11

usually vigorous growth of seedlings in burned areas is often attributed to fertilization by deposited ash and increased mineralization due to soil heating (DeBano *et al.* 1977). Yet, removal of above-ground biomass can also be far more complete after fires than after other disturbances, such as canopy gap formation. As such, it is likely a combination of above- and below-ground effects that make fire a promising management tool for tree species with shade-intolerant regeneration (Hungerford *et al.* 1990, Bond and van Wilgen 1996).

The effects of forest fires on above- and below-ground processes may vary widely depending on their intensity (Moreno and Oechel 1994, Bond and van Wilgen 1996). For example, low-intensity fires may have a positive effect on regeneration by increasing available soil nutrients (DeBano *et al.* 1977, Wright and Bailey 1982), and stimulating flowering (Whelan 1994, LeMaitre and Brown 1992), resprouting (Zedler *et al.* 1983, Moreno and Oechel 1994), and germination of buried seeds (Bradstock and Auld 1995, Schimmel and Granstrom 1996, Enwright *et al.* 1997). In contrast, high-intensity fires may be detrimental to regeneration by volatilizing nutrients (Wright and Bailey 1982), altering soil properties such as texture, cation-exchange capacity, and water holding capacity (DeBano *et al.* 1977, Hungerford *et al.* 1990), killing buried seeds (Schimmel and Granstrom 1996), killing species that would otherwise resprout (Moreno and Oechel 1994), and damaging or killing potential seed trees. Although there is generally a positive relationship between the size or intensity of disturbance and the subsequent availability of resources for plant growth (Canham and Marks 1985) this pattern may not apply for fires of extreme severity. Regeneration on sites of low-intensity fires may be enhanced while areas of high-intensity fire may be very slow to recover.

I designed an experiment to address the relative importance of canopy opening, above-ground biomass removal, and controlled burns of high and low intensity on early patterns of tropical dry forest regeneration. Using these experiments, I examined soil physical and chemical properties (Chapter 3), establishment and growth of commercial tree seedlings (Chapter 4), and

changes in the plant community (Chapter 5), comparing each response to conditions in undisturbed forest understories. In this chapter, I introduce the study site and describe the treatments.

Study Site

The studies described in this dissertation were conducted in the seasonally dry forests of Chiquitania, a geographic region in the eastern lowlands of Bolivia located in the Province of Nuflo de Chavez, Department of Santa Cruz (16°45'S, 61°45'W; Figure 2-1). Chiquitania is situated in a transition zone between the humid forests on the southern rim of the Amazon basin and the thorn scrub formations of the Gran Chaco. The natural vegetation is classified as tropical dry forest (sensu Holdridge *et al.* 1967).

The regional climate is characterized by pronounced seasonality with a strong dry season that corresponds to the austral winter (Figure 2-2). Most of the canopy trees are seasonally deciduous, shedding their leaves from June to September. The mean annual temperature at Concepcion is 24.3°C with temperatures that vary between 3° (July) and 38.1°C (October, Killeen *et al.* 1990). The mean annual precipitation is 1129 mm and interannual variability is large, with lows having reached 500 mm and highs 1717 mm per year (Killeen *et al.* 1990). The landscape is dominated by low hills composed of granite, gneiss, and metamorphic rocks of Precambrian origin (Geobold 1981 in Killeen et al. 1990) punctuated by exposed granitic outcrops (inselbergs). The soils of the area are classified as Inceptisols (suborder: Tropepts, group: Ustropepts) and Oxisols (suborder:Ustox, group: Eutrusox; Ippore 1996). Elevation varies between 400 and 600 m a.s.l.

Canopies of mature forest range from 12-18 m tall and are dominated by trees of the Leguminosae (60% of total basal area of trees >10 cm dbh); trees in the families Bignoniaceae, Anacardiaceae, and Bombacaceae are also abundant (Killeen *et al.* 1998). Understory trees are mostly represented by the families Sapindaceae and Myrtaceae. A spiny ground bromeliad, *Pseudananas sagenarius*, is distributed over approximately 80% of the forest and occurs in clumps up to 2000 m^2 (MacDonald *et al.* 1998).
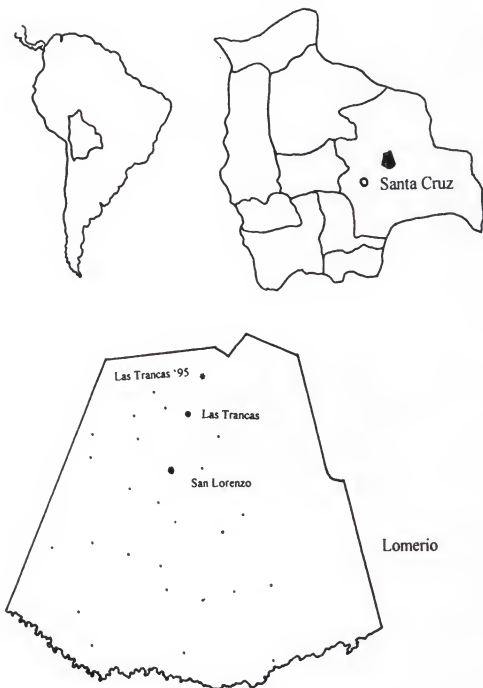
Figure 2-1. Location of the study site in the seasonally dry forests of Chiquitania, a geographic region in the eastern lowlands of Bolivia located in the Province of Nuflo de Chavez, Department of Santa Cruz (16°45'S, 61°45'W). In the enlarged area, points mark the 28 communities in the political region of Lomerio.
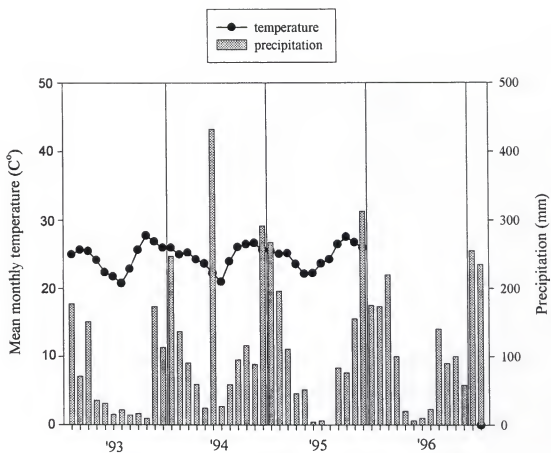
Figure 2-2. Mean monthly temperature and monthly precipitation at Concepcion, Santa Cruz (16°7' S, 62°2' W, 490 m a.s.l.), located approximately 100 km from Lomerio.

Site background

Chiquitania is so named for the Chiquitano indigenous people, the largest of the lowland indigenous groups in Bolivia, with a population of around 72,500. Lomerio, where this study was conducted, is a political region within Chiquitania made up of 27 Chiquitano communities with a total population of around 5,000. The Chiquitanos of Lomerio have been managing their forests for timber since 1982 with technical and financial support from several international institutions. BOLFOR (Proyecto de Manejo Forestal Sostenible), a sustainable forest management project with USAID funding, began working in Lomerio in 1992. The objective of the current management plan for the forests of Lomerio is to produce timber sustainably while minimizing negative impacts on other biological and physical resources in the forest (Pinard *et al.* 1999). Forestry operations of the Chiquitano communities were certified as sustainable by the SmartWood Program of Rainforest Alliance in 1995.

The particular forest in which I worked is owned by the Chiquitano community of Las Trancas and situated approximately 12 km northeast of this village. The Las Trancas forest contains 400 ha management blocks, Las Trancas '94 and Las Trancas '95, so named for the year in which forest inventories were conducted (Figure 2-3). Las Trancas '94 was selectively logged in July-September of 1995. On average, 3-10 m^3 ha^{-1} (2-5 trees ha^{-1}) of timber were extracted from 6 species. Damage to the residual stand was slight, with 6% of the residual trees damaged and 2-4% of the area covered by roads and extraction routes (Camacho 1996). Two logging methods were employed in Las Trancas '95. In 1996, approximately 75% of the area was selectively logged. In 1997, the remaining 25% of the area was selectively harvested in strips (40 m x 200 m, each separated by an unharvested area 60 m wide). All commercially valuable trees were harvested from these strips at a harvesting intensity of 4.4 m^3 ha^{-1}. Log extraction routes (skid trails) entered each logging strip 100 m from the north and 100 m from the south.
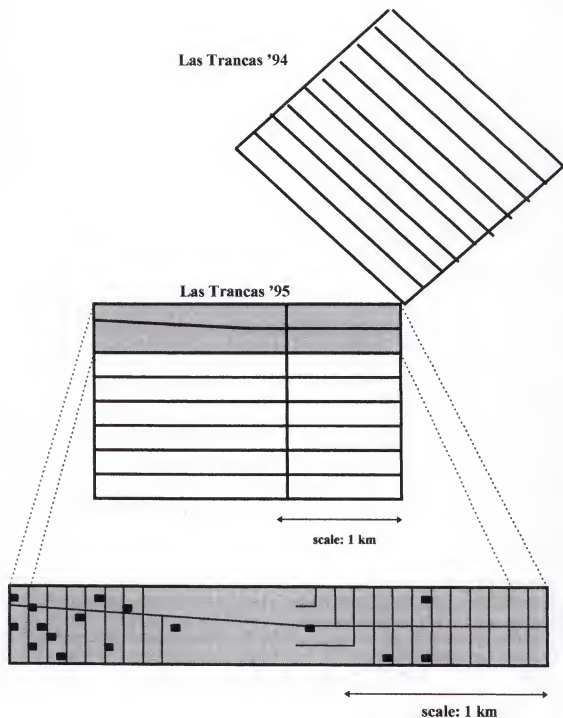
Figure 2-3. The '94 and '95 management blocks of the Las Trancas community owned forest. The enlarged section of Las Trancas '95 represents the trial area for the strip shelter wood system. The squares within this enlarged area mark the 16 blocks (20 x 20 m gap areas) depicted in Figure 2-4.

Methods

Location of felling gaps

The studies presented in Chapter 3, 4, and 5 were conducted in the selectively harvested strips in Las Trancas '95. These strips were the only area of logging activity during the dry season of 1997 and therefore all newly created felling gaps were located in these strips. In June of 1997, I located 16 felling gaps for study (Figure 2-3). Gap selection was restricted by the following criteria: canopy gap area between 200-600 m², slopes no greater than 15°, less than 20% rock outcrops, no trees > 40 cm DBH within gap area, and not located in the path of skid trails.

I located and marked the center of each gap where the midpoints of two perpendicular transects intersected, the first running the length of the longest axis. Each gap was divided into four 10 x 10 m plots by cardinal axes from the center point (Figure 2-4). Half-meter wide paths around the perimeter of the gap and along axes were cut by machete. Existing gap area was enlarged to a uniform 20 m x 20 m area by cutting all vegetation >2 m tall (sensu Brokaw 1985a) by machete or chainsaw. Because this forest is a timber management area, commercial tree species > 20 cm DBH located within the 20 m x 20 m gap area were left uncut (this occurred in only 4 of 16 gaps and standing trees did not exceed 25 cm DBH).

Gap Treatments

One of four treatments was randomly assigned to each 10 x 10 m plot within each block: 1) high-intensity burn; 2) low-intensity burn; 3) plant and coarse debris removal (hereafter referred to as plant removal); and, 4) canopy gap with vegetation > 2 m tall cut (the gap control). Other than cutting all vegetation > 2 m tall, vegetation and woody debris in the gap control was not manipulated. In the plant removal and low-intensity burn treatments, all vegetation was cut at or near the soil surface and everything ≥2.5 cm diameter (≥ 100 hour fuels) was removed and distributed as evenly as possible in the high-intensity burn treatment. Tree trunks and large diameter branches were sawn into smaller sections so that they could be moved more easily and dry
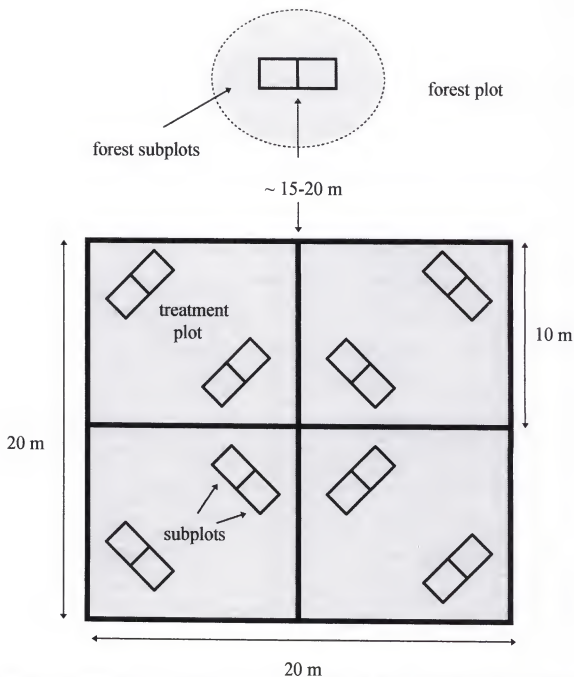
Figure 2-4. A single block consisting of a 20 x 20 m felling gap and an adjacent forest plot. Each felling gap was equally partitioned into four 10 x 10 m treatment plots. Each treatment plot was randomly assigned one of four treatments: gap control, plant removal, low intensity or high intensity burn. Within each treatment plot, 2 permanent vegetation sampling subplots (2 x 2 each) were located near the gap center and 2 additional subplots near the gap edge. All soil sampling was conducted outside of these permanent sampling plots. Two permanent subplots were located approximately 15-20 m from the edge of each gap in undisturbed forest. Soil sampling in the forest was conducted outside but within 5 m of these permanent forest subplots. Hereafter, the 400 m^2 felling gap and adjacent forest site are "blocks," the 100 m^2 treatment areas are "plots," and the 4 m^2 vegetation sampling areas are "subplots."

rapidly. *Pseudananas sagenarius* and cacti were not added to the high-intensity burn treatment, but instead were removed from the block altogether because of their low flammability. Therefore, after fuels were manipulated and before prescribed burns, the plant removal and low-intensity burn treatments had similar amounts of litter and woody debris and no above-ground vegetation. The high-intensity burn treatment plots had roughly 3 times its original fuel load. Slash was left for 5 rainless weeks to dry before prescribed burns were conducted.

Controlled burns

Fuel loads. Pre-burn fuel loads in the low- and high-intensity burn treatments were measured in randomly located 0.25 m^2 circular subplots, with 2 subplots sampled per plot x intensity treatment (2 fuel plots x 2 burn treatments x 16 plots). All fuel within each subplot was removed, divided into fuel diameter size classes (live herbs, <6 mm, 6-25 mm, 25-75 mm, and >75 mm) and weighed in the field. Composite subsamples of each fuel size class were taken from the field, oven dried to constant weight, and used to calculate the wet-to-dry weight conversion factors. The diameter and length of trunks and large diameter branches that could not be weighed in the field were measured in order to estimate volumes. Wood densities available from BOLFOR were used for volume to mass conversions.

Timing of burns. Although little is known about the historic fire regime in these forests, seasonal patterns in rainfall and relative humidity make wildfires most likely at the end of the dry season when fuels are dry and lightning strikes most common. The indigenous Chiquitano population traditionally burn their agricultural fields and cattle pastures at the end of the dry season as well, shortly before the onset of rains. Predictably, most escaped fires occur during this season. Because one of the objectives of my experimental burns was to enhance seedling establishment of commercial tree species, I planned a burning date in late August or early September, at the end of the dry season and before peak seed fall of most commercial trees (Justiniano 1997).

Fire breaks. All fuel was removed from a 1 m wide fire break around low-intensity burn treatment plots. Fire breaks around high-intensity burn treatment plots were 1 to 2 m wide, wider where danger of fire escape was perceived to be higher. Standing dead trees near firebreaks were felled and ladder fuels such as liana tangles were removed. On the day of burns, firebreaks were raked free of newly fallen leaves.

Prescribed burns. Prescribed burns were conducted from August 29 to September 1, 1997, near the end of the 5 month dry season (Table 2-1). Each day, the earliest burns were started at 10:00 a.m. and the last burns by 3:00 p.m. Temperature at 10:00 a.m. over the four day period varied from 34 to 36.4° C and relative humidity varied from 29-38 %. Winds were variable, but usually calm in the morning with convectional wind gusts of up to 11 km/hr in the afternoon.

A circular ignition technique was used for both burn treatments. A spot fire was lit with a drip torch in the plot center, then the perimeter was lit starting with the downwind side. The center fires created convection which drew the ring fire on the borders inward. In the low-intensity burn treatment plots, ring fires often did not carry to the center, therefore spot fires were ignited where needed.

A minimum of 5 people conducted the burns over the 4 day period. At least one person with a backpack water sprayer remained at each fire until fires near the borders were extinguished. Fires near firebreaks or standing dead trees were extinguished before burning crews returned to camp. Each fire was checked again after dark and the following morning to extinguish any potentially dangerous smoldering areas.

Maximum soil temperatures, fire intensities and completeness of burns. Maximum soil temperature and an index of fire intensity were measured in two locations in each burn plot, near the two subplots where fuel loads were measured. Maximum soil temperature was measured at 0 and 3 cm depth using temperature indicating paints (Tempilaq ®, Tempil Division. Air Liquide

Table 2-1. Climatic conditions at 10:00 a.m. the morning of high and low intensity burns for 16 experimental blocks.

Block	Date burned	Ambient temperature (C)	Relative humidity (%)	Wind speed (km/hr)	
1	29-Aug	36	29	0	with gusts
19	29-Aug	36	29	0	with gusts
20	29-Aug	36	29	0	with gusts
4	30-Aug	34	34	11	
6	30-Aug	34	34	11	
8	30-Aug	34	34	11	
21	30-Aug	34	34	11	
22	30-Aug	34	34	11	
2	31-Aug	34	37	4	
7	31-Aug	34	37	4	
9	31-Aug	34	37	4	
11	01-Sep	35	38	0	with gusts
14	01-Sep	35	38	0	with gusts
17	01-Sep	35	38	0	with gusts
18	01-Sep	35	38	0	with gusts

America Corporation, South Plainfield, New Jersey, USA). Paints of 24 different melting points ranging from 66 to 1093° C were applied as narrow bands on 2 x 30 cm steel strips. At each location, one painted steel strip was buried at 3 cm soil depth and another placed flat on the soil surface directly above it. Soil temperatures were measured to a greater depth in one block. Here, an additional 3 sets of 4 painted strips were placed at 0, 1, 3, and 7 cm depths. After fires, the highest indicated melting point was recorded.

Fire intensity was estimated by Beaufait's (1966) technique which calculates total energy output from the amount of water vaporized from cans during burns as:

total energy output = [(80 cal/g water) x (g water)] + [(540 cal/g water) x (g water)]

Where 80 cal are needed to raise each gram of water from 20° C to the boiling point and 540 cal are needed vaporize each gram of water (latent heat of vaporization). Two tin cans per burn were used, each placed on the soil surface of fuel load subplots. Depth of water was measured immediately before each burn and within 24 hours after. To account for the amount of water lost due to evaporation, 2 cans were placed in the center of an unburned gap and the amount of water evaporated within 24-hrs measured.

Soil moisture, which influences heat movement through soil, was measured several hours before burns. Soil samples from 0-5 and 5-10 cm depths were collected from each plot, weighed, oven dried to a constant weight, and moisture content expressed as % of soil dry weight.

The week following burns, completeness-of-burn was estimated visually as the percent area burned

Establishment of permanent vegetation plots

Three weeks following burns, 4 permanent subplots (2 x 2 m each) were established in each treatment plot, 2 located near the gap center and 2 located near the gap edge (Figure 2-4). Two additional subplots were established at random points in undisturbed forest 15-20 m from the edge of each gap. These permanent subplots were used for sampling commercial tree seedling

establishment (Chapter 4) and vegetative cover (Chapter 5). One plot of each pair was used for a seeding treatment described in Chapter 4.

Treatment effects on canopy cover and microhabitat

Soil temperature to 3 cm depth was measured at a center and edge subplot of each treatment as well as the forest subplots with a soil thermometer 3 and 6 months following burns. Percent canopy cover was measured with a spherical densiometer above each gap center, gap edge, and forest plot 3 months following burns. Litter depth (cm) and percent cover by debris 2-20 cm and >20 cm diameter were estimated visually for each of the permanent 4 m^2 subplots 6 weeks following burns. Results were analyzed using an analysis of variance, with treatment as a fixed effect and block as a random effect, followed by Tukey's post-hoc comparisons.

<div align="center">

Initial Treatment Results

</div>

Pre-burn fuel loads

Pre-burn fuel loads in high-intensity burn treatment subplots ranged from 10.8 to 82.8 kg/m^2 and averaged 48 ± 4.9 kg/m^2 (mean $\pm$ 1 standard error; Figure 2-5). Almost half of this mass was comprised of fuels >7.5 cm diameter. Fuel loads in the low-intensity burn treatment subplots ranged from 0.8 to 4 kg/m^2 and averaged 2.2 ± 2.3 kg/m^2. Sixty-six percent of the fuel mass in low-intensity plots was fine fuel, <6 mm diameter.

Burn characteristics

High-intensity burns. Completeness of high-intensity burns was variable, but the majority of burns consumed all but the thickest (> 20 cm diameter) branches and trunks. Flame heights ranged from 1.5 to 5 m. Fire intensities ranged from 152 to 3795 kcal and averaged 1627 ± 241 kcal (n = 15). Temperature at the soil surface during high-intensity burns averaged 704 ± 42 °C (n = 16). The highest temperature measured was 927° C. Temperature at 3 cm depth averaged 227 ± 27 °C (n = 16). Where maximum temperature was measured at additional depths of 1 and 7
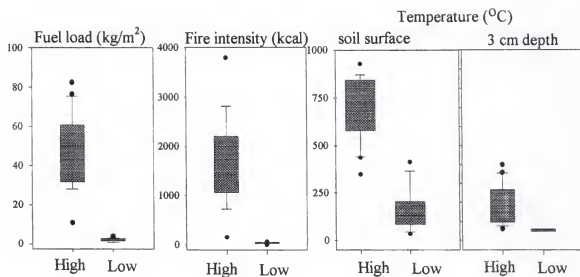
Figure 2-5. Pre-burn fuel loads, fire intensities, and maximum temperatures at the soil surface and 3 cm depth during high and low intensity burns. Box plots show medians (center line), 25th and 75th percentiles (top and bottom lines), 10th and 90th percentiles (top and bottom whiskers), and points greater than the 90th percentile and less than the 19th percentile (dots).

cm, temperatures averaged 871 °C at the soil surface, 358 °C at 1 cm depth, 218 °C at 3 cm depth, and 135 °C at 7 cm depth (n = 2). Although visible flames were extinguished by nightfall, some logs continued to smolder for several days; fire intensities and soil temperatures under these logs were likely greater than measured values.

Low-intensity burns. In general, completeness of low-intensity burns was more variable than high-intensity burns. Flame heights were low, ranging from 10 to 50 cm. Fire intensity ranged from 22 to 68 kcal and averaged 41 ± 3 kcal (n = 15). Temperatures at the soil surface averaged 225 ± 33 °C (n = 12); the highest temperature measured was 413 °C. Elevated temperatures at 3 cm were only detected in 2 of 16 plots; these averaged 107 ± 7 °C (n = 2). Soil moisture on the day of burns was low and did not differ between the high- and low-intensity burn plots (0-5 cm depth: $P = 0.94$, 5-10 cm depth: $P = 0.23$). Therefore, differences among the 2 burn treatments in heat conductivity due to soil moisture were likely negligible and are hereafter ignored.

Treatment effects on microhabitat

Treatments had significant effects on the amount of soil exposed, mid-day ambient soil temperature, litter depth, and area covered by woody debris (Figure 2-6). Canopy cover above forest plots was 78%, higher than canopy cover above all 4 gap treatments, which averaged 22% ($P < 0.001$). Although canopy cover above gap-center and gap-edge plots was not significantly different ($P = 0.6$), soil temperatures in gap centers were higher than near gap edges ($P < 0.001$). A maximum temperature of 43° C was recorded in the center of one high-intensity burn treatment 3 months following burns. After 6 months, soil temperatures at gap centers and edges were not different ($P = 0.52$) and only soil temperatures in the high-intensity burn treatment were significantly higher than the other treatments ($P < 0.001$).

High-intensity burns removed all litter and deposited a layer of ash ranging from 0-14 cm depth (4.8 ± 0.2 cm, n = 16). Not all woody material was consumed in the high-intensity burns;
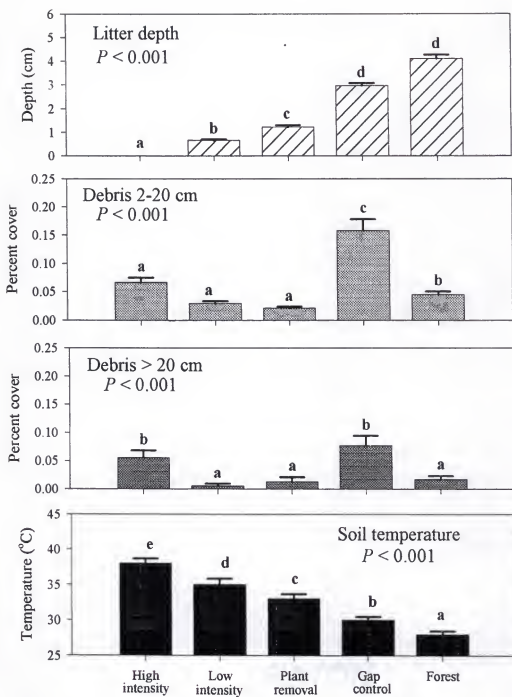
Figure 2-6. Litter depth, percent cover of debris 2-20 cm and > 20 cm diameter, and mid-day soil temperature in four gap treatment plots and forest plots 6 weeks after burns. Treatments with the same letter are not significantly different.

the remaining woody debris covered approximately 12% of the subplots areas. In the low-intensity

burn treatment, an average of 76% of the subplot areas burned to some degree. Burning was not

complete even within these areas as only an average of 30% of the subplot areas had soil exposed.

Small woody debris remained on approximately 3% of the area of low-intensity burn subplots;

most large woody debris had been removed before burning.

Leaf litter or small woody debris covered all of the plant removal treatment subplots, with

no bare soil exposed. As with the low-intensity burn treatment, most large woody debris was

removed. Gap controls were characterized by deep leaf litter (2.9 ± 0.2 cm, $n = 16$) and small and

large woody debris covering an average of 25% of the subplot areas. Only 20% of the gap control

subplot areas were devoid of either woody material or surviving plants. Forest understories had

the deepest leaf litter (4.0 ± 0.3 cm, $n = 16$), but small and large woody debris combined covered

an average of only 7% of the subplot areas.

CHAPTER 3
EFFECTS OF CANOPY GAP FORMATION, PLANT REMOVAL,
AND CONTROLLED BURNS OF HIGH AND LOW INTENSITIES ON
SOIL CHEMICAL AND PHYSICAL PROPERTIES

Introduction

Fire is a rapid decomposer; it compresses the oxidative processes of organic matter decay into a short time span (Wright and Bailey 1982). The result is a nutrient pulse much larger than from the normal decomposition of woody debris and litter, at least for the first few months following fires (Bond and van Wilgen 1996). As such, controlled burns may benefit tree seedling growth more than unburned treatments, particularly since the timing of nutrient pulses following fire coincides with maximum light availability. After intense fires, however, the advantages of increased nutrient availability may be offset by degraded soil structure. Thus, the benefit of controlled burns for tree seedling growth may ultimately depend on fire intensity. In this chapter, I examine both soil nutrient availability and soil physical properties following canopy opening, plant removal, and controlled burns of high- and low-intensity.

There are three primary mechanisms of increased nutrient availability following fire: nutrients added to the soil as ash; heating of soil organic matter; and, increased rates of biological mineralization following fire due to increases in soil pH, temperature, and moisture, as well as due to a reduction in C:N ratios (Wright and Bailey 1982, Pritchett and Fisher 1987). The degree of increase in nutrient availability following fires depends largely on fire intensity. Most studies of low to moderately intense fires report increases in available nutrients (reviews by Dunn *et al.* 1977, DeBano *et al.* 1977, Wells *et al.* 1979, Humphreys and Craig 1981, Wright and Bailey 1982,

Hungerford et al 1990, Neary *et al.* 1999). In contrast, intense fires may cause a net loss of nutrients (DeBano *et al.* 1977, Giovannini *et al.* 1990).

Due to its low temperature of volatilization (200° C; Weast 1988), nitrogen loss is linked with the consumption of organic matter (e.g., Dunn et al. 1977). Where fuels are completely consumed and the surface layer of soil organic matter is destroyed, loss of nitrogen through volatilization can be substantial (e.g., Nye and Greenland 1964, Ewel *et al.* 1981). Volatilization of phosphorus and cations are usually minor due to the high volatilization temperatures of these minerals ($>760^\circ$ C; Weast 1988), however, their loss from severely burned sites may be caused by surface erosion, leaching, or transport of ash (Wright and Bailey 1982).

Intense burns may also have detrimental effects on soil physical properties by consuming soil organic matter. Soil organic matter holds sand, silt, and clay particles into aggregates, therefore a loss of soil organic matter results in a loss of soil structure. Severe fires may also permanently alter soil texture by fusing clay particles into sand-sized particles (Dyrness and Youngberg 1957, Ulery and Graham 1993). By altering soil structure and texture, severe fires can increase soil bulk density (DeByle 1981), and reduce soil porosity, water infiltration rates, and water holding capacity (e.g., Wells *et al.* 1979). Intense burns may also induce the formation of a water repellent soil layer by forcing hydrophobic substances in litter downward through the soil profile (DeBano 1969), reducing water infiltration rates as a consequence (DeBano 1971).

The changes in chemical and physical soil properties caused by fire potentially have important consequences on tree seedling growth (Johnson 1919). Increased nutrient availability after fire may benefit plant growth if nutrients are limiting prior to burning (e.g., Hungerford *et al.* 1990). On the other hand, seedling growth in intensely burned soils may be slowed due to high pH and toxic levels of minerals (Giovannini *et al.* 1990). Altered soil physical properties, such as soil strength, bulk density, and water infiltration rates, may also impair plant growth. Plant uptake of nutrients and water is slowed in structurally degraded soils through the combined effects of lower

soil moisture and lower soil porosity (Nye and Tinker 1977). Mechanical impedance of root growth caused by increased bulk density and soil strength (Gerard *et al.* 1982) also slows nutrient and water uptake.

In this chapter, I focus on the below-ground effects of the treatments described in Chapter 2. My objectives were to: 1) compare the effects of canopy gap formation, plant removal, and controlled burns of high and low intensities on soil nutrient availability, soil physical properties, and fine root mass; 2) compare the relative importance of soil heating and ash-fertilization on soil nutrient availability; and, 3) discuss how these treatment-induced changes in soil properties influence tree seedling growth.

Methods

Study site

The studies presented in this chapter were conducted in the treatment and forest plots described in Chapter 2 (Figure 2-4). All soil sampling was done within the 100 m^2 plots but outside of the 4 m^2 subplots. Forest sampling was done within 5 m of the forest subplots.

Mass and chemical characteristics of ash deposited in high-intensity burn plots

Ash mass deposited in high-intensity burn plots was estimated by collecting and weighing all ash on the soil surface in a 1 m^2 area, replicated in three high-intensity burn plots (n = 3). To characterize variability in the amount, ash depth was measured in 10 randomly located points in each high-intensity burn plot (n = 16). Composite ash samples were then collected from each plot and used to measure pH and nutrient concentrations. Ash pH was determined as for soil pH, described below. To determine nutrient concentrations, 0.5 g of ash was heated in 10 mL of 1 M HNO_3 and then resolubilized in 10 mL of 1 M HCl. Extracts were then analyzed for phosphorus, potassium, calcium, and magnesium at the Analytical Research Laboratory at the University of Florida with an ICAP Spectrometer (Thermo-Jarrell Ash Corporation, Franklin, MA).

Soil sampling

Soil samples from 0-8 cm depth were collected 2, 6, 9, 12 and 18 months after burns and from 8-20 cm depth after 9, 12, and 18 months. These samples were used to assess moisture contents, pH, organic matter, and extractable elements. In each treatment and forest plot (n = 16 blocks), 4 samples were taken from randomly selected sites with a 10 cm diameter cylindrical corer. The 4 samples from each treatment were mixed thoroughly in the field and a ~300 g composite subsample bagged (Anderson and Ingram 1993). In one block, the 3-month samples were bagged separately, rather than composited, to examine intra-treatment variability. Subsample soil volume was unknown, therefore bulk density and fine root mass were sampled separately as described below.

Soil pH and air-dry moisture content

The pH of fresh soil was determined by adding 50 ml of distilled water to 20 g of soil and stirring for 10 minutes (Anderson and Ingram 1993). The mixture then stood for 30 minutes and pH of the supernatant was measured with a hand-held meter (Oakton® pHTestr 3). Soil samples were then weighed, air-dried to a constant weight, and reweighed to calculate air-dry moisture content. Air-dried samples were passed through a 2 mm sieve, bagged, and stored in a cool dry area until transported back to the Analytical Research Lab at the University of Florida for chemical analyses.

Soil chemical analyses

Phosphorus, potassium, calcium, and magnesium were extracted with Mehlich-I solution: 0.05 M HCl and 0.0125 M H_2SO_4 (Hanlon *et al.* 1994). Extracts were then analyzed by ICAP spectroscopy. Soil organic matter content was analyzed using the Walkley-Black dichromate methodology (Hanlon *et al.* 1994). A subset of soil samples was tested for total nitrogen using an elemental analyzer (Carloerba NCS 2500). Twenty-four samples from all treatments and sampling periods from the top 8 cm of soil were selected to represent the full range of organic matter content.

Resin-available nitrogen and phosphorus

Resin-available nitrogen (NH_4^+-N and NO_3^--N) and phosphorus (PO_4^{-3}-P) in each treatment were estimated by burying anion and cation exchange resin bags at 5 cm depth. Resin bags were prepared by enclosing 5.0 g (moist weight) of either anion exchange resins (Sigma-Dowex®) or cation exchange resins (Fisher Scientific®) in bags of nylon stocking material sewn closed with nylon thread. Before burial, resin bags were hydrated overnight with dionized water. Four bags of each resin type were buried per treatment plot (4 bags x 2 resin types x 5 treatments x 16 blocks). Three rotations of resins were buried, each for approximately 3 months. Two rotations included the first and second rainy seasons following burns (November 1997-January 1998 and December 1998-February 1999, respectively). The middle rotation covered the transition from the first rainy season to the first dry season following burns (May-July 1998). After removal from the field, resin bags were placed separately in clean plastic bags and kept cool (refrigerated when possible) until transported to the University of Florida for analysis. For each resin type, the 4 bags per plot were pooled and 12 g extracted in 120 ml of 2 M KCl for 24 hours. Extractions were analyzed for amonium-N and nitrate-N using automated spectrophotometry (Flow IV Ion Analyzer, AlpKem (O-I-Analytical), College Station, TX). Extracts from anion exchange resins were diluted to 1M KCl and analyzed for PO_4^{-3}-P using the atomic emission spectrometric method (Thermo-Jarrell Ash Corp, Franklin, MA).

Statistical analyses

Soil nutrient concentrations, organic matter, pH, moisture content, and resin-available N and P were analyzed using an ANOVA with repeated measures. Treatment was a fixed effect and block a random effect in each model. Soil properties were log transformed for analyses when not normally distributed, but all values presented in the text are non-transformed. Where a significant time x treatment interaction was found, variables were analyzed separately by month. Statistically significant differences ($P < 0.05$) were further analyzed with Tukey's HSD multiple comparisons.

In order to describe variation within plots, 4 soil samples per treatment in one block (block 4) were analyzed separately for extractable nutrients and organic matter. Also, 4 resin bags per treatment in one block were extracted and analyzed separately for resin-available nitrogen and phosphorus. Coefficients of variation (Sokal and Rohlf 1981) were calculated to compare variation of soil sampled within the same 100 m^2 plot and among the 16 different plots.

Fine root mass

Fine root mass (roots < 2 mm diameter) was compared among treatments 12 months following burns in a reduced sample of 10 blocks (n = 10). Soil cores were extracted with a cylindrical tube (5 cm inside diameter, 7 cm deep) from 3 randomly located points in each treatment and forest plot. Fine roots were sorted from samples, dried, and weighed. Fine root mass (live and dead combined) was compared among treatments using an ANOVA followed by a Tukey's HSD post-hoc test.

Soil bulk density

Soil bulk density (air-dry) was estimated 6 and 12 months following burns in a reduced sample of 10 blocks (n = 10). Three samples in each treatment and forest plot were collected using metal cans (5 cm inside diameter, 7 cm deep, 137 cm^3). Samples were air-dried to constant weight and bulk density calculated as:

$$\text{bulk density (g/cm}^3) = \text{g air-dried soil / 137 cm}^3$$

Differences among treatments were tested using an ANOVA on square-transformed values of bulk density with treatment and month as fixed effects and blocks as a random effect, followed by Tukey's HSD multiple comparisons.

Soil strength

Compressive soil strength was estimated with a pocket penetrometer (Forestry Suppliers®) at 2, 6, 9, and 12 months following burns. Soil strength readings were taken at 4 randomly selected points in each treatment and forest plot from all 16 blocks (n = 16). Soil strength was

analyzed using ANOVA with repeated measures as described above for soil chemical properties.

Water infiltration

Water infiltration rates were estimated in a reduced sample of 4 blocks 8 months following burns (n = 4). The technique used here was a modified version of the single ring method (Anderson and Ingram 1993). Although double ring methods provide better estimates of infiltration rates because they compensate for lateral flow, a single ring method was chosen for this study because it used less water (which had to be transported 27 km). In each gap treatment and forest site, a point was randomly located and cleared of surface litter. A graduated PCV cylinder (10 cm diameter, 25 cm length) was inserted vertically into the soil 10 cm deep and soil pressed around the base to minimize water leakage. The cylinder was filled with water to 10 cm and timed until the water level dropped to 5 cm. This process was repeated three times. Infiltration rates were calculated separately for each repetition (i.e., the first, second, and third 5 cm increments of water which correspond to 5, 10, and 15 ml cm^{-2}) as the volume flux of water flowing into the soil profile per unit surface area (Hillel 1982) and expressed as ml cm^{-2} sec^{-1}. Log transformed infiltration rates were compared among treatments using an ANOVA with treatments and repetitions (i.e., each 5 cm increment) as fixed effects and blocks as random effects.

Soil wettability

Soil wettability was estimated using a modification of the water drop penetration time method (WDPT; Letey 1969) in a reduced sample of 7 blocks 8 months following burns (n = 7). In each gap treatment and forest site, four 20 x 20 cm areas were randomly located and cleared of surface litter. Five drops of water were placed on the soil surface with a dropper and the time recorded when all 5 drops were completely absorbed. This was repeated at 1, 2, and 3 cm soil depth by scraping surface soil away with a machete. Soil wettability (log transformed seconds) was compared among treatments using an ANOVA with treatments and soil depth as fixed effects and blocks as random effects.

Comparative effects of soil heating and ash addition on soil chemical properties

To compare the effects of soil heating and ash addition on soil chemical properties, I carried out a 2 x 3 factorial experiment with two levels of ash addition (no ash and ash added) with three levels of soil heating (no heat, low-intensity heat, and high-intensity heat). The first trial was conducted in the field in Las Trancas '95. The second trial was conducted in the BOLFOR greenhouse in the city of Santa Cruz. *Anadenanthera colubrina* served as a bioassay in the field experiment. Because *Anadenanthera* did not fruit in 1998, *Caesalpinia pluviosa* was used as a bioassay in the greenhouse study.

Field study. I utilized the plant removal treatment plots described in Chapter 2 for the field study, conducted at the end of the dry season in October 1997. The design is a complete randomized block; each plant removal plot was considered as a block (n = 12). In each block, six 1 m^2 plots were located in the area between the gap center and edge permanent subplots (Figure 2-4). Competing vegetation had been cleared from the larger treatment plots the month before, but some regrowth had already occurred. Therefore the 1 m^2 plots were cleared again of any vegetation and raked of surface litter to expose the soil surface. Each plot was randomly assigned a treatment combination of soil heating (no heat, low-intensity heat, or high-intensity heat) and ash (no ash or ash added). Treatments were applied to a 50 x 50 cm area in the center of the 1 m^2 plots, creating a 25 cm buffer along the edge. Heat was applied using a propane blow torch. Temperature of the flame was measured with Tempil® heat sensitive paints. In the low-intensity heat treatment, a flame of 150-250°C was applied to the soil surface of the treatment area for 5 minutes. In the high-intensity heat treatment, a flame of 500-800°C was applied to the soil surface of the treatment area for 20 minutes. The torch required constant adjustment to maintain a similar flame, therefore temperatures varied within a treatment. I am confident, however, that temperatures ranges did not overlap between the high- and low-intensity treatments. After heat

treatments, approximately 500 g of ash collected from high-intensity burn plots was distributed as evenly as possible to plots assigned the ash treatment. The week following treatments, 10 seeds of *Anadenanthera colubrina* were placed in each plot and checked for germination after 4 days. After 2 weeks, most seeds were found to have been removed or eaten and were therefore not checked again.

Soil samples 0-8 cm depth were collected 3 weeks following treatments. Soil pH, and phosphorus, potassium, calcium, magnesium, and organic matter concentrations were analyzed using the methods described above. Resin-available nitrogen (NH_4^+-N and NO_3^--N) was measured using anion and cation exchange resin bags. One bag of each type was buried at 5 cm depth in each plot for 85 days (October 31 - January 24). Analysis of resins follows that described for the larger study.

Greenhouse study. The greenhouse study was conducted at the end of the dry season in 1998. Soil used for this trial was collected from Las Trancas '95 to a depth of 10 cm. Soil was passed through an 8 mm sieve, mixed well, and divided into three equal batches. Each batch was assigned a soil heating treatment (no heat, low-intensity heat, and high-intensity heat). In the low-intensity heat treatment, soil was heated in aluminum pots in a conventional oven at 100-150° C for a total of 10 minutes (mixing after 5 minutes). Soil in the high-intensity treatment was oven heated at ~200° C for 40 minutes (mixing after 20 minutes) then spread 1 cm deep on a metal tray and heated with a blow torch for 5 minutes at a temperature of 500-800° C. Oven temperature and torch temperature were both measured using Tempil® heat sensitive paints. One composite soil sample from each heating treatment (control, low-intensity, and high-intensity) was analyzed for phosphorus, potassium, calcium, magnesium, and organic matter concentrations. Soil from each heating treatment was used to fill 24 plastic planting containers (7 x 25 cm). Twelve planting containers per heating treatment were then selected for the ash addition treatment (15 g of ash

added to the soil surface) and the remaining 12 containers served as controls (n = 12). Two seeds of *Caesalpinia pluviosa* were placed in each planting container, watered daily, and seedling height to the terminal bud was measured after 4 months. Resin-available nitrogen (NH_4^+-N and NO_3^--N) was measured in each treatment combination using additional planting containers. Anion and cation exchange resin bags were buried at 5 cm depth in 3 containers of each treatment combination (n = 3) and watered daily for 22 days. Resins were extracted and analyzed using the methods described above.

Results

Mass and chemical characteristics of ash deposited in high-intensity burn plots

Variability in amount of deposited ash was high and depths ranged from 0-14 cm (4.8 ± 0.3 cm, x ± S.E., n = 16). Ash mass deposited by high-intensity burns averaged 1.5 ± 0.6 kg/m^2 (n = 3). Using this value and measured concentrations of individual elements in ash (Figure 3-1) indicates an average nutrient deposition of 524 g/m^2 of Ca, 26 g/m^2 of Mg, 83 g/m^2 of K, and 7.7 g/m^2 of P. Ash samples had an average pH of 10.7 ± 0.1 (n = 16).

Treatment effects on soil nutrients

High-intensity burns significantly increased P, Mg, K, and Ca in the top 8 cm of soil, but the magnitude and its change over time varied by nutrient (Figure 3-2). These increases were also detected at 8-20 cm for all elements except Mg (Figure 3-3). Low-intensity burns also significantly increased P, Mg, K, and Ca in the top 8 cm of soil, although increases were smaller than in high-intensity burn plots, did not persist as long, and were not detected at 8-20 cm. Plant removal and gap control treatments had no detectable effect on P, Mg, K, and Ca at either soil depth. Results of statistical analyses are summarized in Tables 3-1 and 3-2.
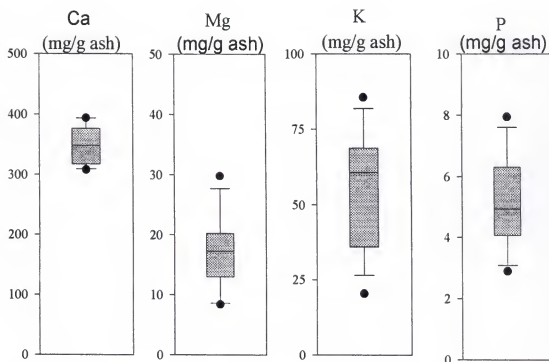
Figure 3-1. Box plot diagrams of concentrations of Ca, Mg, K, and P in ash sampled from high intensity burn plots (n = 9). Box plots show medians (center line), 25th and 75th percentiles (top and bottom lines), 10th and 90th percentiles (top and bottom whiskers), and observations lying outside of the 10th to 90th percentiles (dots).
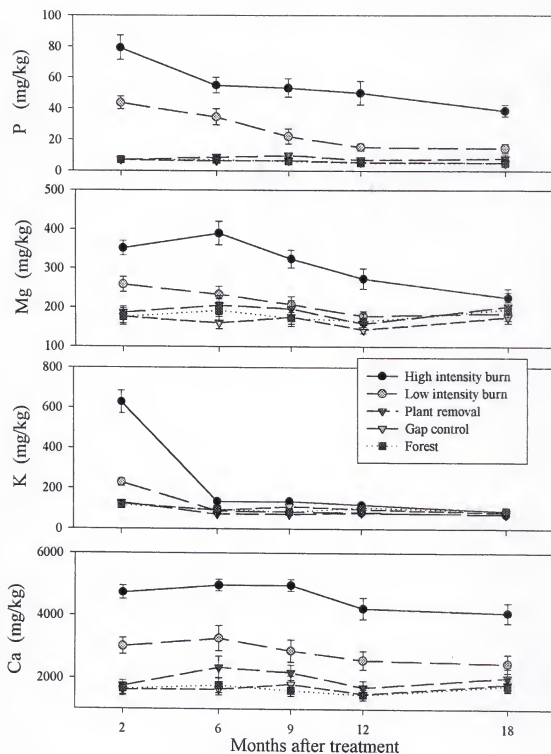
Figure 3-2. Extractable soil concentrations of P, Mg, Ca, and K in soil samples (0- 8 cm depth) in four gap treatments and forest sites at 5 sampling times over an 18 month period following burns (bars = S.E.).
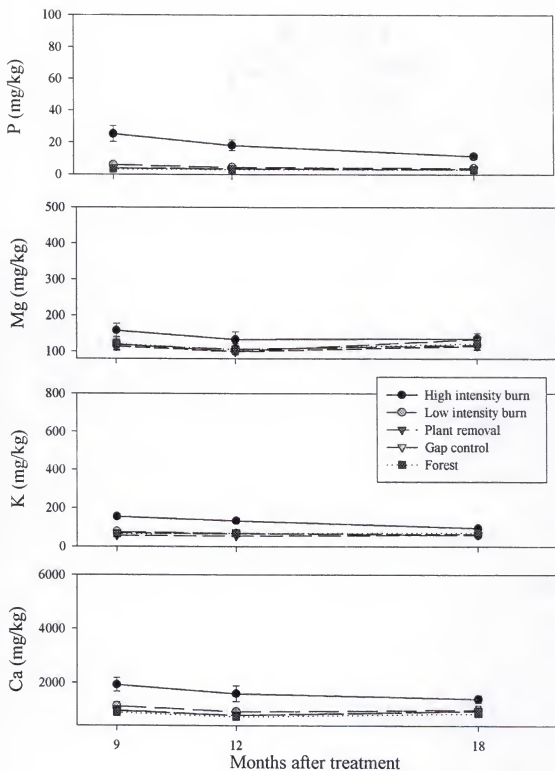
Figure 3-3. Extractable P, Mg, K, and Ca in soil sampled from 8-20 cm in four gap treatments and forest sites at 9, 12, and 18 months following burns. Y-axis scales are identical to those in Figure 3-2 for soils sampled from 0-8 cm depth (bars = S.E.).

Table 3-1. Results of ANOVAs of soil nutrients, organic matter, water content, and soil pH of soil sampled 0-8 cm in four gap treatments and forest plots at 5 times following burns. All variables were log transformed. Where a significant time * treatment interaction was found, variables were analyzed separately by month. Treatments with different letters are significantly different at P < 0.05.

| No interaction time * treatment | | | | | Post-hoc test results | | | | |
Variable	Factor	F	P	Month	high	low	removal	control	forest
Magnesium	Treatment	23.3	< 0.001	3	a	b	c	c	c
	Time	8.7	< 0.001	6	a	b	bc	c	c
				9	a	b	bc	c	c
				12	a	b	c	c	c
				18	a	b	b	b	b
Calcium	Treatment	70.1	< 0.001	3	a	b	c	c	c
	Time	3.0	0.026	6	a	b	bc	c	bc
				9	a	b	b	b	b
				12	a	b	b	b	b
				18	a	a	a	a	a
Water content	Treatment	3.9	0.008	3	ab	a	a	a	b
	Time	39.0	< 0.001	6	ab	ab	a	ab	b
				9	a	a	a	a	b
				12	a	a	a	a	a
				18	a	a	a	a	a

| Significant time * treatment interaction | | | | | Post-hoc test results | | | | |
Variable	Month	F	P		high	low	removal	control	forest
Potassium	3	77.4	< 0.001		a	b	c	c	c
	6	64.1	< 0.001		a	bc	c	bc	b
	9	11.5	< 0.001		a	bc	c	b	bc
	12	7.8	< 0.001		a	b	b	ab	a
	18	3.7	0.009		ab	b	b	ab	a
Phosphorus	3	167.5	< 0.001		a	b	c	c	c
	6	60.8	< 0.001		a	a	b	b	b
	9	45.5	< 0.001		a	b	c	c	c
	12	58.7	< 0.001		a	b	c	c	c
	18	37.2	< 0.001		a	b	c	c	c
Organic matter	3	7.3	< 0.001		a	b	b	b	b
	6	15.9	< 0.001		a	b	b	b	b
	9	4.6	0.003		a	b	b	ab	ab
	12	4.7	0.002		a	b	ab	ab	b
	18	3.9	0.007		ab	ab	b	ab	a
Soil strength	3	12.6	< 0.001		a	b	b	b	b
	6	24.3	< 0.001		a	a	a	b	c
	9	28.8	< 0.001		a	b	b	c	c
	12	16.9	< 0.001		a	bc	b	c	c

Table 3-2. Results of ANOVAs of soil nutrients, organic matter, water content, and soil pH in the 8-20 cm depth of soil of four gap treatments and forest plots at 3 times following burns. All variables were log transformed. Where a significant time * treatment interaction was found. variables were analyzed separately by month. Treatments with different letters are significantly different at P < 0.05.

No interaction time * treatment							Post-hoc test results		
Variable	Factor	F	P	Month	high	low	removal	control	forest
Phosphorus	Treatment	105.4	< 0.001	9	a	b	bc	bc	bc
	Time	59.4	< 0.001	12	a	b	bc	bc	bc
				18	a	b	b	b	b
Magnesium	Treatment	2.1	0.09	9					
	Time	7.3	0.001	12					
				18					
Calcium	Treatment	10.5	< 0.001	9	a	b	b	b	b
	Time	4.7	0.013	12	a	ab	b	b	b
				18	a	b	ab	b	b
Water content	Treatment	5.6	0.001	9	a	a	a	a	b
	Time	51.2	< 0.001	12					
				18	ab	ab	a	ab	b
pH	Treatment	70.9	< 0.001	9	a	b	bc	c	bc
	Time	58.9	< 0.001	12	a	b	c	c	c
				18	a	b	c	c	c

Significant time * treatment interaction						Post-hoc test results		
Variable	Month	F	P	high	low	removal	control	forest
Potassium	9	34.6	< 0.001	a	b	c	bc	bc
	12	17.5	< 0.001	a	b	b	b	b
	18	9.5	< 0.001	a	b	b	b	b
Organic matter	9	1.7	0.16					
	12	2.7	< 0.001	a	ab	ab	b	ab
	18	11.3	< 0.001	b	b	a	c	c

Total soil N was strongly related to soil carbon ($R^2 = 0.93$; Figure 3-4) thus, patterns of total N differences among treatments are expected to follow those for soil organic matter.

Both high- and low-intensity burn treatments significantly increased resin-available NH_4^+-N, NO_3^--N, and PO_4^{-3}-P during the first rainy season following burns (Table 3-3, Figure 3-5). This pulse decreased after the first rainy season. Other than an increase in NO_3^--N in plant removal treatments during the first rainy season, the remaining treatments had little effect on NH_4^+-N, NO_3^--N, and PO_4^{-3}-P availability.

Coefficients of variation (CV) calculated for soil nutrients and organic matter within one plot and among the 16 plots for each treatment are displayed in Table 3-4. A pattern emerged that in the burned treatments, soil nutrients and organic matter were more variable within the one plot than among all 16 plots. The opposite pattern was true for the plant removal, gap control, and forest plots. Variation was in general greater among the 16 different plots than within the one plot.

Treatment effects on soil pH, soil organic matter content, and soil water content

Soil pH after high-intensity burns at 0-8 and 8-20 cm was higher than in all other treatments throughout the 18 month sampling period (Figure 3-6 and 3-7). Soil pH in high-intensity burn plots was 2 pH units higher than forest soils 2 months following burns. In low-intensity burn treatments, pH was higher than in the remaining treatments at both depths at all sampling periods. The plant removal and gap control treatments had little effect on soil pH.

High-intensity burn treatments significantly lowered soil organic matter; 2 months following high-intensity burns soil organic matter in the top 8 cm of soil was approximately 72% that of forest soils. By 18 months soil organic matter recovered to levels comparable to the remaining treatments. Differences among the remaining treatments were small and varied throughout the sampling periods.
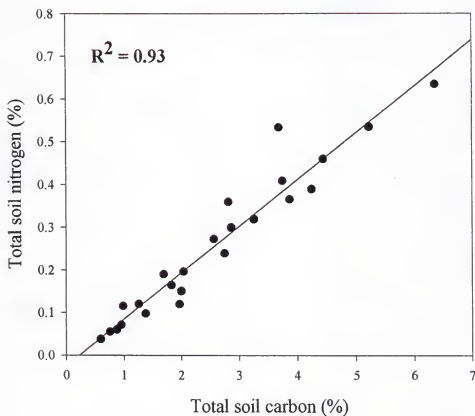
Figure 3-4. Total soil nitrogen and soil carbon in soil sampled 0-8 cm depth. Soil samples used for this analyses were chosen from among all treatments and all times since burns (2, 6, 9, 12, and 18 months) to obtain as wide a range as possible for carbon content.

Table 3-3. Results of ANOVAs of resin exchangable NH_4, NO_3, and PO_4 in 4 gap treatment and forest plots measured at 3 time periods following burns. All variables had a significant time*treatment interaction and therefore all were analyzed separately by month. All variables were log transformed prior to analyses. Treatments with different letters are significantly at $P < 0.05$.

Variable		Analyzed by time period		Post-hoc test results				
		F	*P*	high	low	removal	control	forest
NH_4-N	first wet season	58.7	0	a	b	c	c	c
	first dry season	11.2	0	a	a	ab	bc	c
	second wet season	2	0.11					
NO_3-N	first wet season	6.3	0	a	ab	ab	b	b
	first dry season	4.5	0.003	ab	a	a	ab	b
	second wet season	9.9	0	a	ab	bc	bc	c
PO_4-P	first wet season	12.2	0	a	a	b	b	b
	first dry season	12.2	0	a	bc	c	b	ab
	second wet season	3.2	0.02	a	bc	ab	ab	ab
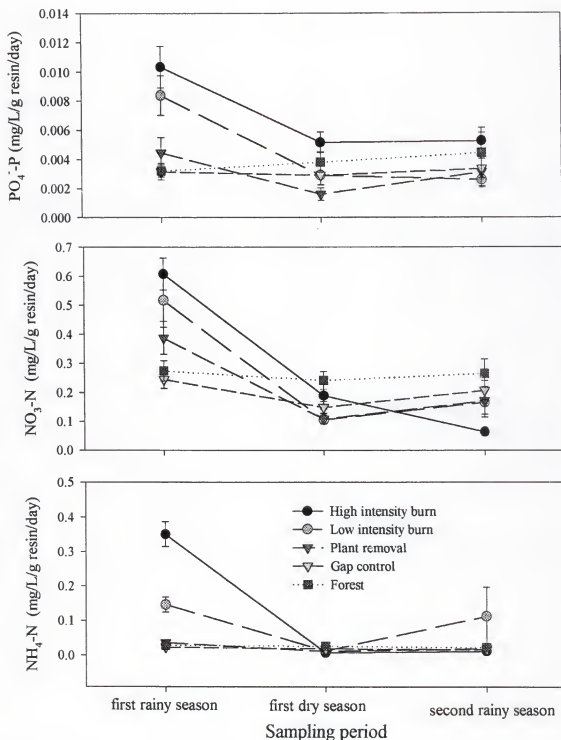
Figure 3-5. Resin-available ammonium, nitrate, and phosphate determined from exchange resins buried in soil at 5 cm depth during 3 periods following treatments. Resins were buried for approximately 3 months during each period. Time since burn of sampling periods were: 1st rainy season (2-5 mo), 1st dry season (8-11 mo), and 2nd rainy season (15-18 mo; bars = S.E.).

Table 3-4. Coefficients of variation[a] (CV) of soil cations, organic matter, and resin-available nitrogen sampled within a 100 m² plot ("within") and among the 16 different plots ("among") of each treatment. CV within plots was calculated from 4 samples taken from each treatment in one block. CV among plots was calculated from the composite samples taken from each treatment of 16 blocks. All calculations were performed with data taken 3 months following burns.

	High intensity burn		Low intensity burn		Plant removal		Gap control		Forest	
	within	among	within	among	within	among	within	among	within	among
Ca	39 *	18	42 *	35	28	37	15	53	36	46
Mg	40 *	36	53 *	32	19	22	7	31	17	35
K	47 *	21	53 *	30	34 *	31	21	49	17	39
P	84 *	39	66 *	38	8	27	23	29	14	54
OM	33 *	24	37 *	20	24	25	8 *	35	24 *	19
NO₃-N	27	36	25	71	49	58	75 *	51	48	51
NH₄-N	49	160	54 *	39	41	114	53 *	18	41 *	20
ash depth	46 *	22								

[a] CV = (standard deviation / mean) * 100 (Sokal and Rohlf 1981)

* = coefficient of variation greater within a single treatment plot than among all treatment plots.
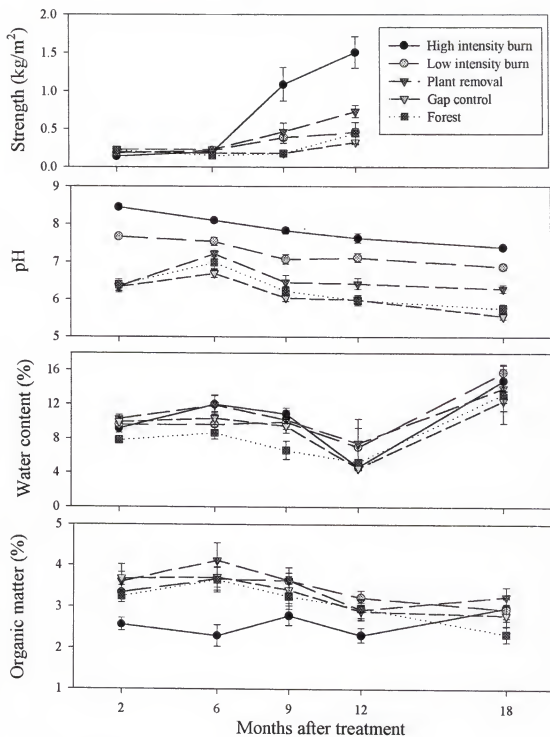
Figure 3-6. Soil pH, air-dry water content, and organic matter content measured in soil (0-8 cm depth) in the four gap treatments and forest sites at 5 sampling times over an 18 month period following burns. Soil strength was measured at the soil surface with a soil penetrometer at 4 sampling periods over a 12 month period following burns. Water content is expressed as a percentage of air-dry weight (bars = S.E.).
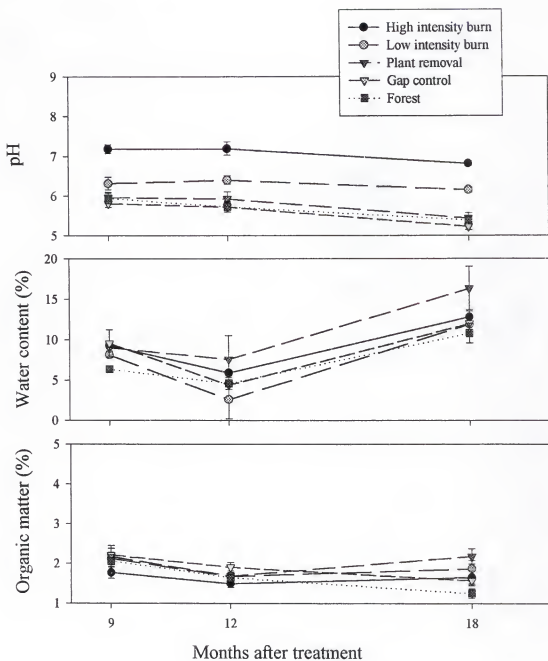
Figure 3-7. Soil pH, air-dry water content, and organic matter content in soil sampled from 8-20 cm depth in four gap treatments and forest sites at 9, 12, and 18 months following burns. Y-axis scales are identical to those in Figure 3-6 for soil sampled from 0-8 cm depth (bars = S.E.).

Although significant differences in soil water content were detected among treatments, differences were not large and patterns were not consistent over the sampling period. The forest plots had the lowest soil water content during the first 9 months, but this difference diminished after 12 months. Larger differences were due to seasonal changes in soil water content, predictably with the highest water contents in the rainy season of 1999, and the lowest water contents in the dry season of September 1998.

Treatment effects on fine root mass

Fine root mass 18 months following burns was significantly higher in forest plots than in high- and low-intensity burn treatments ($F = 4.4$, $P = 0.005$, $n = 10$). Fine root mass (live and dead combined) in the top 7 cm of soil in was: forest 1.8 ± 0.3 kg/m^2, gap control 1.3 ± 0.2 kg/m^2, plant removal 1.3 ± 0.2 kg/m^2, low-intensity burn 0.9 ± 0.1 kg/m^2, and high-intensity burn 0.7 ± 0.1 kg/m^2.

Treatment effects on soil physical properties

Soil bulk density and soil strength. Bulk density in high-intensity burn treatments was significantly higher than in forest plots after 6 and 12 months ($F = 3.1$, $P = 0.02$, $n = 10$). There were no significant differences among the remaining treatments. Bulk density averaged 1.3 ± 0.05 g cm^{-2} in high-intensity burn treatments and 1.2 ± 0.02 g cm^{-2} in forest plots after 12 months.

Soil strength in high-intensity burn treatments increased during the first 12 months following burns (Figure 3-6, Table 3-1). Although at 3 months, soil strength was lowest in high-intensity burn treatments, it was the highest in this treatment by 9 months. Soil strength in the other treatments also increased during the first 12 months, but to a less extent than in high-intensity burn plots.

Water infiltration and soil wettability. Water infiltration rates were significantly lower in the high-intensity burns than in the remaining treatments ($F = 31$, $P < 0.001$, Figure 3-8). Soil

wettability significantly differed among treatments (F = 4.6, P = 0.002) and a slight, but non-significant, difference was found in the wettability of different soil depths (F = 2.4, P = 0.07). Surface soils in all treatments except the high-intensity burn tended to repel water (Figure 3-9). In the high-intensity burn treatment, a slightly water-repellent layer was detected at 2-3 cm depths.

Effects of soil heating and ash addition on soil chemical properties

Field study. Due to high seed predation of *A. colubrina*, I only report results of soil analyses. Ash addition significantly increased soil concentrations of P, K, Ca, and Mg as well as soil pH (Table 3-5; Figure 3-10). Ash addition lowered soil organic matter, but did not affect available resin-available NH_4^+-N and NO_3^--N. Heated soil had lower concentrations of Mg, but did not have significantly different concentrations of P, K, Ca, organic matter, or resin-available NH_4^+-N and NO_3^--N.

Greenhouse study. Both soil heating and ash addition decreased growth of *C. pluviosa* seedlings (Table 3-6; Figure 3-11). Intensely heated soil had higher levels of resin-available NH_4^+-N than moderately heated or control soil. Resin-available NO_3^--N was not detectable in intensely heated soil, but it was significantly higher in moderately heated soil than control soil. Ash addition did not affect resin-available NH_4^+-N and NO_3^--N.

Discussion

Effects of high- and low-intensity burns on soil chemical properties

Controlled burns significantly affected on all soil chemical properties examined (soil pH, soil organic matter, resin-available N and P, and Mehlich-extractable P, Ca, K, and Mg). These changes, attributable to soil heating and/or ash deposited during burns, were greater after high-intensity burns than low-intensity burns. High fuel loads combined with relatively complete burns in the high-intensity burn treatment resulted in an average ash depth of 4.8 cm. Maximum temperatures reached during high-intensity burns averaged 704°C at the soil surface and 227°C at 3 cm depth (Chapter 2). Little ash was deposited after low-intensity burns, due mostly to the lower
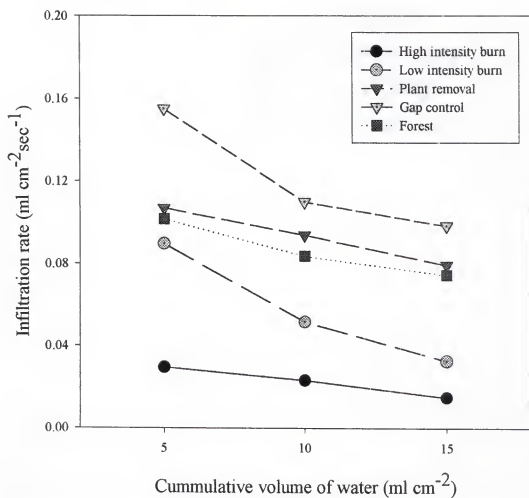
Figure 3-8. Water infiltration rates of soil in four gap treatments and forest plots. Infiltration was measured as the time required for the first 5 ml of a 10 ml column of water to infiltrate soil.
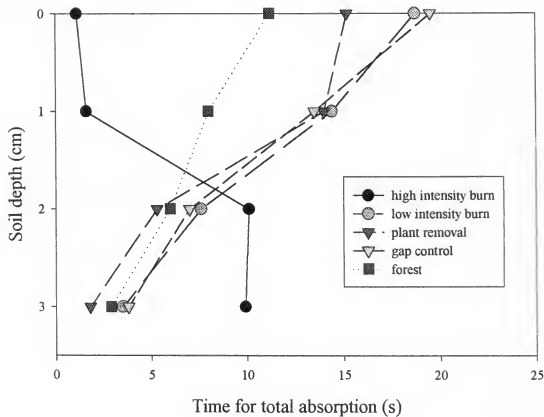
Figure 3-9. Soil wettability at the soil surface soil and at 1, 2, and 3 cm depths in four gap treatments and forest plots. X-axis refers to the time to total aborption of 5 drops of water applied to the soil surface with a dropper.

Table 3-5. Results of ANOVAs of a field experiment examining the separate effects of ash addition and soil heating on soil properties. Two levels of ash (no ash, 500 g ash) and 3 levels of soil heating (no heat, low intensity heat, and high intensity heat) were applied to 0.25 m^2 subplots in the field and soil sampled after 3 weeks. In the low intensity heat treatment, a flame of 150-250°C was applied to the soil surface of the treatment area for 5 minutes with a propane torch. In the high intensity heat treatment, a flame of 500-800°C was applied to the soil surface of the treatment area for 20 minutes. Ammonium and nitrate were measured using anion and cation exchange resins buried at a depth of 5 cm for 3 months (n = 12).

| | | Factors | | | | | |
| | | Ash | | Heat | | Ash * heat | |
Variable	df	F	P	F	P	F	P
Calcium	15	615.8	< 0.001	3.1	0.05	3.3	0.05
Potassium*	15	65.5	< 0.001	1.2	0.32	0.5	0.59
Magnesium*	15	75.6	< 0.001	4.7	0.01	1.0	0.38
Phosphorus*	15	23.5	< 0.001	0.2	0.81	2.8	0.07
NH$_4$-N*	15	2.7	0.11	1.3	0.29	0.4	0.96
NO$_3$-N*	15	1.2	0.28	1.8	0.17	2.3	0.11
OM	15	11.7	0.001	3.8	0.03	2.3	0.11
pH	15	210.3	< 0.001	2.7	0.08	0.4	0.96

* log transformed prior to analyses
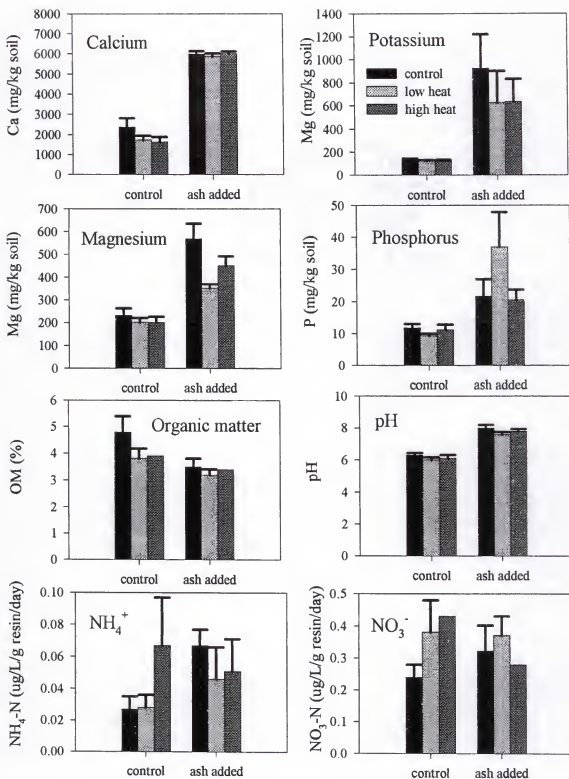
Figure 3-10. Results of field study of soil that had received combinations of heating (no heat, low intensity heat, and high intensity heat) and ash addition (no ash, ash added). All soil was sampled from 0-8 cm depth, 3 weeks after treatments. Resin available NH_4^+ and NO_3^- were measured using anion and cation exchange resins buried to a depth of 5 cm for 3 months (n=12; bars=S.E.).

Table 3-6. Results of ANOVAs of a greenhouse experiment examining the separate effects o ash addition and soil heating on available nitrogen and seedling growth of *Caesalpinia pluviosa*. Two levels of ash (no ash, 15 g ash added) and 3 levels of soil heating (no heat, lov intensity heat, and high intensity heat) were applied to soil used to fill planting bags. In the lov intensity heat treatment, soil was heated in a coventional oven at 150-200° C for 10 minutes. In the high intensity heat treatment, soil was heated in a coventional oven at ~250° C for 40 minutes and fired with a propane torch for 5 minutes at a flame temperature of 500-800° C. Ammonium and nitrate weremeasured using anion and cation exchange resins buried at a dept of 5 cm for 3 months. Seedling height was measured 4 months after planting (n = 12).

		Factors					
		Ash		Heat		Ash * heat	
Variable	df	F	P	F	P	F	P
NH_4-N	5	6.2	0..023	291.0	< 0.001	1.8	0.20
NO_3-N	5	1.7	0.20	23.3	< 0.001	0.6	0.58
Seedling height						4.8	0.012**

**Significant interaction for seedling height therefore analyzed separately by heat treatment.

	Heat treatment	F	P	tallest
Seedling height	no heat	11.4	0.003	w/o ash
	low heat	11.7	0.002	w/o ash
	high heat	0.15	0.7	
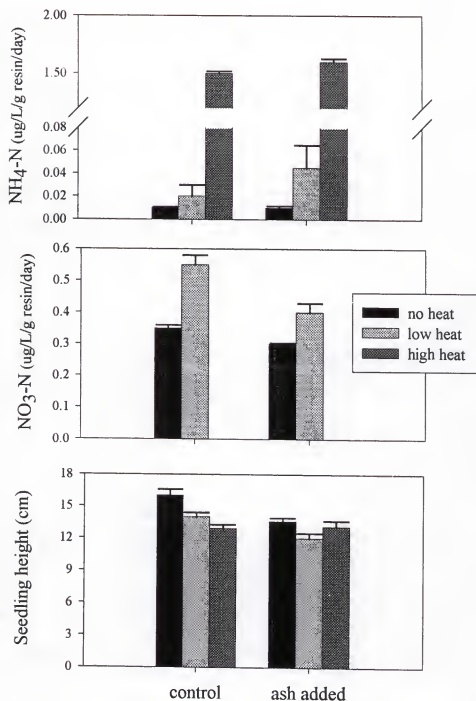
Figure 3-11. Results of greenhouse study of *Caesalpinia pluviosa* seedlings planted in soil that been heated (no heat, low intensity heat, and high intensity heat) and had ash added (no ash, 15 g ash added). Seedling height was measured 4 months after planting (n = 12). Ammonium and nitrate were measured using anion and cation exchange resins buried in individual bags and watered for 22 days (n = 3). Bars are S.E.

fuel loads but also to incomplete combustion of these fuels. Maximum temperatures reached during low-intensity burns averaged $225°C$ at the soil surface; elevated temperatures at 3 cm depth were mostly undetectable.

Soil pH. Increased soil pH is a general effect forest fires (e.g., DeBano *et al.* 1977, Wright and Bailey 1982, Kutiel *et al.* 1990, Hungerford *et al.* 1990, Stromgaard 1992, Neary *et al.* 1999). High concentrations of basic cations in ash deposited following fires (e.g., Ca, K, Mg, Na) is the major mechanism of increased soil pH (Kutiel *et al.* 1990, Stromgaard 1992). Although soil heating may also increase pH by releasing basic cations from soil organic matter (Giovannini *et al.* 1990), results of the soil heating and ash addition field study (Figure 3-11) revealed that ash addition significantly increased soil pH while soil heating had only a slight but non-significant effect.

Soil organic matter. High-intensity burns caused a net loss of organic matter in surface soils, a predictable consequence of intense fire (e.g., DeBano et. al. 1977, Hungerford *et al.* 1990, Neary *et al.* 1999). Several studies conducted in the tropics have found decreased soil organic matter following slash burning (Amazonia: Uhl and Jordan 1984, Mackensen *et al.* 1996, Australia: Rab 1996). Experimental studies have shown that soil organic matter loss is a direct effect of soil heating (e.g., Hosking 1938, in Humphreys and Craig 1981, Giovannini *et al.* 1990), with distillation of volatile organic compounds occurring between soil temperatures of $100\text{-}300°C$ and near complete loss of soil organic matter at temperatures $>450°C$. Soil organic matter contents following high-intensity burns (Figure 3-6), averaged over 0-8 cm, likely do not reflect larger losses in soil organic matter that occurred in the first several centimeters. Consumption of soil organic matter was probably complete at the soil surface during the high-intensity burns, where maximum soil temperatures averaged $683°C$. Due the sharp decrease in soil temperature with depth (Chapter 2), organic matter consumption was probably negligible below the top several cm of soil and not detected at 8-20 cm depth.

Average surface temperatures during low-intensity burns (160° C) were not hot enough for the consumption of soil organic matter, hence average soil organic matter contents of low-intensity burn plots were not significantly lower than those of forest soils. In fact, average soil organic matter contents after low-intensity burns were higher than those of adjacent forest soils. Increases in soil organic matter have been shown to occur during light to moderate burns (e.g., Hungerford *et al.* 1990) due to the incorporation of unburned or partially burned slash fragments into soil. For example, Stromgaard (1992) attributed increased soil carbon following slash burning in miombo woodlands to charcoal accumulation or small organic particles washed in from ash.

Soil organic matter in high-intensity burn plots recovered to levels higher than those in forest plots within 18 months following burns. High daytime soil temperature in burned plots and high soil moisture within gap treatments may have contributed to this rapid recovery by increasing decomposition rates. Though generally rapid, recovery of soil organic matter following slash and burn vary among and within tropical forests. For example, at the same site in the Venezuelan Amazon, Montagnini and Buschbacher (1989) reported recovery of soil organic matter within 6 months, while Uhl and Jordan (1984) reported that recovery required 5 years. Other than differences in climate and site productivity, fire intensity and land use following burns also affect recovery of soil organic matter, thus making comparisons among studies difficult.

Total soil nitrogen. Total soil N was linearly related to soil organic carbon, hence the greatest declines in soil N occurred in high-intensity burn plots where organic matter in the top 8 cm of soil decreased an average of 28% from adjacent forest soils. Similarly, total soil N was reported to decrease following slash and burn of tropical forest in Costa Rica (Ewel *et al.* 1981) and in the Venezuelan Amazon (Uhl and Jordan 1984). As with soil organic matter, this average (28%) underestimates N losses from the top several centimeters of soil or from more intensely burned patches; N losses reached 84% in the top 8 cm of soil and likely approached 100% in scorched surface soils. Comparably high N losses were reported in chaparral soil heated to 500° C

(80% N loss; Dunn and DeBano 1977) and Mediterranean soils heated to 600° C (86% N loss; Kutiel *et al.* 1990).

Losses of total soil N during low-intensity burns were negligible as indicated by low losses of soil organic matter. In fact, slightly higher soil organic matter contents in low-intensity burn plots relative to adjacent forest soil suggest that total soil N increased after this treatment. This is likely due to the mixing of slash fragments into surface soils. Increases in total N in surface soils has also been found following slash burning in the tropical forests (Montagnini and Buschbacher 1989, Stromgaard 1992) and temperate forests (Gholz *et al.* 1985).

Resin-available nitrogen. In contrast to decreases in total soil N, amounts of resin-available nitrogen (NH_4^+-N and NO_3^--N) increased after burns of high-intensity. These findings agree with those of Matson *et al.* (1987) and Montagnini and Buschbacher (1989), who also reported increases of ammonium and nitrate following slash burning of tropical forest in Costa Rica and Venezuela, respectively. In the present study, low-intensity burns increased resin-available N levels as well, although to a lesser degree than high-intensity burns. Temperate zone studies have also noted that increases in inorganic N are dependent on fire intensity (Dunn and DeBano 1977, Giovannini *et al.* 1990, Kutiel *et al.* 1990, Rice 1993, Weston and Attiwill 1996, McMurtrie and Dewar 1997). Dunn and DeBano (1977) demonstrated that the greatest increases in ammonium and nitrate for chaparral soils occurred at soil temperatures up to 300° C, due to the mineralization of organic N. At soil temperatures of >500° C, inorganic N decreases due to volatilization (Dunn and DeBano 1977). Similar results were reported in soil heating studies conducted by Giovannini *et al.* (1990).

Increased ammonium availability following burns may be enhanced by soil microbial death, which occurs at temperatures as low as 50°-121° C (Neary *et al.* 1999). Soil microbial death was likely substantial in high-intensity burn plots and may have occurred within small well-burned patches in low-intensity burn plots as well. In their study of nitrogen transformations

following slash and burn on volcanic soils in Costa Rica, Matson *et al.* (1987) found that the amount of nitrogen that disappeared from microbial biomass after burns was similar to the concurrent increase in apparent net nitrogen mineralization.

Matson *et al.* (1987) also attributed increased nitrate concentrations to enhanced nitrification rates. Burning generally creates favorable conditions for nitrification, such as raised pH values and base saturation (Pritchett and Fisher 1987). Increased nitrification rates were also reported following slash burning of Venezuelan forests (Montagnini and Buschbacher 1989). In contrast, other studies have shown that nitrification rates are reduced by fire, due to a decreased biomass of nitrifiers (e.g., Dunn and DeBano 1977, Stromgaard 1992). Reduced nitrification rates would cause an accumulation of ammonium, which is less subject to leaching than nitrate. This effect may explain why nitrate was undetectable in the intensely heated soil of the greenhouse study while levels of ammonium were very high (Figure 3-12).

Elevated concentrations of ammonium and nitrate following high and low-intensity burns were short-lived in my study. Within 8 months of burns (after the first rainy season), inorganic N in burned plots declined to levels found in adjacent forest. This result is similar to the rate of decline of inorganic N following slash burning of a wet forest in Costa Rica (Matson *et al.* 1987).

Phosphorus. High- and low-intensity burns increased both extractable P and resin-available PO_4^{-3}-P. Inorganic P additions in ash likely contributed to these increases. In the soil heating and ash addition field study (Figure 3-11), ash addition significantly increased extractable P, while soil heating had little effect. Similarly, Stromgaard (1992) attributed increases in extractable P after slash burning of miombo woodlands to ash deposition, and Rice (1993) found that soil PO_4^{-3}-P concentrations in Californian chaparral following fire were correlated with ash depth but not fire intensity.

Though possibly less important than ash deposition, soil heating can increase extractable P by mineralizing organic P, as may have occurred with resin-available N. Giovannini *et al.* (1990)

found an increase in inorganic P accompanied by an equivalent decrease in organic P in soil samples heated to 460° C; at temperatures >460°C, all organic P was destroyed and only inorganic P remained. Soil heating may have been comparatively more important in low-intensity burn treatments, where relatively little ash was deposited. Other studies have reported increases in inorganic P following fires of low-intensity. For example, in a study of soil nutrient levels associated with shifting agriculture in the Asian tropics, Andriessse and Koopmans (1984) found available P increased almost 300% after heating to 200° C, which they attributed to mineralization of organic P.

Cations. High-intensity burns significantly increased soil concentrations of extractable cations (Ca, K, and Mg). Low-intensity burns also increased cation concentrations, although not as dramatically. Similar to P, results of the soil heating and ash addition field study suggest that increases in extractable cation concentrations by burning is mostly due to ash deposition. Significant increases in extractable Ca, Mg, and K after fire in miombo woodland (Stromgaard 1992) and Brazilian cerrado (Coutinho 1990) were also attributed to ash deposition.

As with P, soil heating may also increase extractable Ca, K, and Mg through mineralization of organic forms (Giovannini et al. 1990). Extractable Ca and Mg peaked in soil heated to 200° C and declined at higher temperatures; extractable K peaked in soil heated to 700° C (Giovannini et al. 1990). Results of the soil heating and ash addition study conform with this pattern; soil heating significantly decreased extractable Ca and Mg concentrations and had no effect on extractable K concentration.

Decreases in cation concentrations over the 18 month post-burn period are similar to those following burns in temperate forests (e.g., DeBano et al. 1977, DeRonde 1990, Kutiel and Shaviv 1992, Hernandez et al. 1997) and tropical forests (e.g., Uhl and Jordan 1984, Coutinho 1990, Stromgaard 1992, Mackensen 1996). The order of decrease (K> Mg > Ca) corresponds with cations' mobility and susceptibility to leaching. In high-intensity burn plots, plant uptake was

probably not important in cation decreases during the first year, as plant cover remained less than 25% (Chapter 5). Plant uptake may have been more important during the second year, as vegetative cover reached 60% after 18 months.

Variation of soil nutrients within and among plots. Based on the comparison of one plot. soil nutrients and organic matter in burned treatments appeared to be more variable within plots than among plots of the same treatment (Table 3-4). This pattern suggests that natural variation in soil nutrients was increased due to heterogeneity of burns. The opposite pattern was true for the plant removal, gap control, and forest plots. Variation in soil properties was in general greater among the 16 different plots than within the same 100 m^2 plot, suggesting variations in soil fertility in the absence of fire are expressed at larger scales.

Actual variation in soil properties after high-intensity burns may have been greater than reflected by random sampling. For example, nutrient and organic matter contents of severely scorched soil differed greatly from averages of high-intensity burn plots. Mineral concentrations of such scorched soil sampled to 5 cm (with percentages of high-intensity burn plot averages) were: 6415 mg/kg Ca (133%); 197 mg/kg Mg (56%); 71 mg/kg K (11%); 0.25 mg/kg P (0.3%); and 0.1% organic matter (4%). These extremely scorched soils were not common (< 1% high-intensity burn plots), but potentially affect plant colonization by providing microsites different from less intensely burned areas.

Increased soil heterogeneity after burns has been observed by other authors. Christensen (1985) noted that soil nutrient concentration in chaparral is considerably more variable after fire than before, due to local variation in fire intensity and the uneven distribution of ash. Heterogeneity in soil nutrients potentially has important consequences for colonizing plants. For example, Rice (1993) observed that even small scale patterns in fire intensity and ash distribution were reflected in later establishment of chaparral shrubs.

Changes in fine root mass following burns

Lower fine root biomass after high-intensity burns was likely due to a combination of rapid decomposition of dead roots as well as direct oxidation by fire. Experimental studies have shown that fine roots are desiccated or killed at soil temperatures of 48°-54°C (Neary *et al.* 1999). Temperatures in high-intensity burn plots (61°-399° C at 3 cm depth) were not only well above this range, but were likely high enough in places to completely oxidize fine roots. Even during low-intensity burns, temperatures in surface soils (160° C average at soil surface) were sufficiently high to kill fine roots. Fine root mortality during burns was likely greater than death of larger roots, not only because of their small size, but also due to their concentration near the soil surface.

Fine root mortality potentially has important effects on soil fertility, as their decomposition may increase soil nutrient concentrations. Nutrient input from roots has been hypothesized to be an important pathway for nutrient cycling, particularly in tropical dry forests, due to their larger store of biomass below-ground (Martinez-Yrizar 1996, Jaramillo and Sanford 1995). Decreased fine live-root mass is also expected to contribute to higher water and nutrient availability due to reduced uptake. However, average soil moisture contents in high-intensity burn plots were not significantly different than those in other gap treatments. Possibly, lower water uptake was offset by decreased water holding capacity of intensely burn soil caused by a loss of soil organic matter.

Effects of high- and low-intensity burns on soil physical properties

Changes in soil strength, bulk density, and water infiltration rates in high-intensity burn plots were substantial. The decrease in soil organic matter in high-intensity burn plots likely influenced these observed changes in soil physical properties. Organic matter influences soil structure through aggregate formation; a decrease in organic matter decreases total porosity, particularly macro-pore spaces (> 0.6 mm). The increase in surface soil strength during the first year following high-intensity burns was likely due to the settling of soil minerals and ash into

spaces left void by organic matter and fine roots. This settling of soil particles would also contribute to higher soil bulk densities.

Decreased macro-pore space would also contribute to the lower infiltration rates observed in high-intensity burn plots. However, these lowered infiltration rates caused by high-intensity burns did not result in any observable surface runoff. The lowest infiltration rate recorded in a high-intensity burn plot was 5 times faster than the rate needed to absorb a 5 cm hr^{-1} rainfall (0.002 cm^{3}cm^{-2}sec^{-1}). Further, most plots were located on level ground, therefore if a rain event exceeded the soil's rate of infiltration, the accrued water would not run-off.

Increased wettability of surface soils after high-intensity burns conforms to studies that report soil temperatures >288°C destroy water-repellent layers (Neary *et al.* 1999). Soil temperatures of 176-288°C reportedly form water-repellent layers (Neary *et al.* 1999), explaining the presence of a slightly water-repellent layer at 2-3 cm depth. However, the decreased wettability of this soil layer does explain the lower infiltration rates in high-intensity burn treatments, as surface soils in the remaining treatments had similar wettability properties. Possibly, a more water-repellent layer was formed deeper than 3 cm in high-intensity burn plots, but was undetected due to the sampling strategy.

Soil strength, bulk density, water infiltration, and water repellency of low-intensity burn plots were not different from those in the unburned treatments. Again, this pattern may reflect the influence of organic matter on soil physical characteristics; the lower temperatures during low-intensity burns (mean 120°C), did not decrease soil organic matter.

Potential effects of high- and low-intensity burns on tree seedling growth

Soil heating and ash addition significantly affected *Caesalpinia* seedling growth, although in a manner opposite than expected; ash addition decreased seedling growth. This result suggests that the quantity of ash added to soil may have been at toxic levels for this species. Also, tree seedlings were shorter in soil heated at both low and high intensities. This result only partially

corresponds with a similar study by Giovannini *et al.* (1990), which examined the effects of soil

heating on wheat (*Triticum aestivum*) seedling growth. They found that while soil heated to 170°

C had no effect on plant growth, soil heated to 220° C and 460° C increased seedling height and

biomass, whereas soil heated to 700° C and 900° C had detrimental effects on seedling growth.

The authors attributed increased growth in moderately heated soil to greater ammonium and

available phosphorus concentrations. Lowered growth in intensely heated soil was attributed to the

sharp increase in soil pH and release of Ca and K to toxic levels, as seedlings in this treatment of

their study showed symptoms of nutritional disorder.

In my greenhouse study, decreased seedling growth in intensely heated soil may be the

result of degraded soil structure or toxic levels of cations. However, it is unclear why seedling

growth was impaired in the lightly heated soil. It is important to consider that although seedling

heights significantly differed among treatments, maximum height differences were only 3 cm. This

slight difference after 4 months of growth may not be biologically significant. Perhaps the effects

of soil heating and ash addition on seedling growth would have been more apparent if a shade-

intolerant species had been used as a bioassay. *Caesalpinia* is partially shade-tolerant and

exhibited slow growth rates in the field as well (Chapter 4).

Despite the potentially negative effects of increased bulk density and soil strength, lowered

infiltration rates, and possibly toxic effects of cations on plant growth, seedling heights of shade-

intolerant species were greatest in high-intensity burn plots (Chapter 4). This increased growth in

intensely burned soils may be due to several factors. Initially, soil strength in high-intensity burn

plots was the lowest of all treatments, therefore early colonizing seedlings should not have

experienced mechanical impedance of root growth. Secondly, nutrient concentrations were highest

in high-intensity burn plots which may have offset decreased movement of nutrients through the

soil. Also, toxic levels of cations may only have been a factor in small areas of high ash deposition

or severely scorched soils; seedlings may not have been able to establish in these small areas and

therefore the effects on growth were not observed. Most importantly, the density of plants colonizing high-intensity burn plots was low (Chapters 5), so that established tree seedlings likely benefited from reduced competition for soil water and nutrients.

Effects of plant removal and canopy gap formation on soil chemical and physical properties

Soil moisture content was higher in all of the gap treatments than forest plots for the first 9 months following burns. Higher soil moisture within tree fall gaps than under adjacent forest is a pattern repeatedly found in tropical forest studies (e.g., Vitousek and Denslow 1986) and has been attributed to decreased transpiration within gaps due to less vegetation. The difference in soil moisture content between forest and gap plots diminished over the first year as the amount of vegetation in gaps increased.

Plant removal and gap control treatments did not significantly change soil chemical or physical properties from those in adjacent intact forest. Although it is hypothesized that the increased soil temperatures, moisture, and litter depth in tree fall gaps will increase nutrient availability (i.e. Bazzaz 1980), conclusive evidence to suggest this is true has not been reported. For example, in a study of natural tree fall gaps in lowland moist forest in Costa Rica, Vitousek and Denslow (1986) found that nitrogen mineralization did not increase in tree fall gaps and slight phosphorus increases were not significant. The only difference they detected was within gap microhabitats; the root throw zone had significantly less N and P than the crown zone. Luizao *et al.* (1998) found similar results in a study of artificial gaps ranging in size from 40-2500 m^2 in Brazilian rain forest. No differences in microbial biomass, soil respiration, and nitrogen mineralization or nitrification were found between gap and forest sites.

Most of the variation observed within the plant removal, gap control, and forest plots over time was due to seasonal changes. Soil moisture content varied predictably with changes in rainfall and NO$_3^-$ availability declined slightly during the dry season. This observation agrees with the few studies of nutrient cycling conducted in tropical dry forests which have shown that nitrification

rates are highest during the rainy season and lowest at the end of the dry season (Singh *et al.* 1989,

Garcia-Mendez *et al.* 1991, see also Smith *et al.* 1998).

Longer term effects of controlled burns on soil properties

The duration of this study limits its conclusions to only short-term treatment effects. A

similar study conducted in Las Trancas in 1995 (Stanley 1995) however, reveals slightly longer

term effects of burning on these forest soils. Although not identical, the treatments applied in this

earlier study were comparable to those used in mine: a gap control; gap vegetation slashed and

removed; gap vegetation slashed and burned; and gap enlarged by 30%, vegetation slashed, and

burned (Stanley 1995). Fires in the enlarged gaps were likely more intense than fires in gaps that

were not enlarged, due to a greater amount of fuel. I measured soil nutrient concentrations and soil

pH at 0-8 and 8-20 cm depths in April 1998, 3 years following experimental burns and found no

significant differences among gap treatments at either depth (Figure 3-12). The soil property with

the most distinct trend was P concentration ($P = 0.11$), followed by Ca concentration ($P = 0.19$),

soil pH ($P = 0.22$), K concentration ($P = 0.27$), Mg concentration ($P = 0.32$), and organic matter

content ($P = 0.35$).

These results suggest that soil chemical changes following burns are relatively short-lived.

However, the lack of significant results may have been more indicative of the large variation found

within treatments rather than the lack of variation found among treatments. Felling gaps included a

diverse array of habitats, such as rock outcrops and stream side areas. Importantly, there was no

indication of declining soil nutrient concentrations in the cleared and burned areas of this pilot

study after 3 years. A widely held notion about the recovery of tropical ecosystems following

disturbance is that severe nutrient losses following deforestation limit forest regeneration (e.g.,

Allen 1985, Buchbacher *et al.* 1988). Clearly, longer-term sampling of the burned plots is needed

before conclusions can be drawn about the long-term sustainability of severely burned soils at this

forest site.
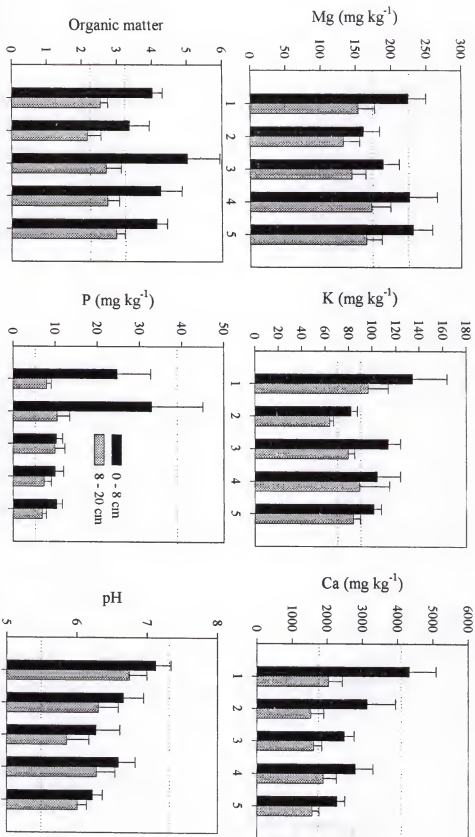
Figure 3-12. Concentrations of extractable Mg, K, Ca, and P, and percent organic matter, and soil pH of soil sampled from logging gaps with the following treatments: 1) enlarged and burned, 2) burne, 3) slash removed, 4) control, and, 5) forest understory. These treatments were applied (3 yrs prior to sampling) to 6 gaps each in Las Trancas '94. Soil was sampled 0-8 cm (black bars) and 8-20 cm (gray bars). Dotted lines represent the range of means of soil sampled from all treatments in my study 18 months following treatments (n = 6; bars = S E.).

Conclusions

The experimental burns had mixed effects on physical, chemical, and biological soil properties. High-intensity burns increased levels of available nitrogen and phosphorus, but these pulses quickly decreased. Ash deposited after high-intensity burns increased cation concentrations, but these pulses declined over time as well. Loss of organic matter during high-intensity burns likely altered surface soil structure. This effect was apparent in increased bulk density and soil strength, and decreased infiltration.

Low-intensity burns increased cation concentrations and available forms of N and P. Soil structural changes were not as marked as after high-intensity burns, because little soil organic matter was consumed. Therefore, soil chemical properties can be altered during low-intensity fires, but changes in soil physical properties may only occur during intense fires. Plant removal, gap control, and forest plots had no significant effects on soil chemical or physical properties.

Greenhouse studies suggested that loss of soil structure caused by soil heating and toxic levels of cations created by large quantities of ash may hinder tree seedling growth. However, these potentially negative effects were not apparent in the field. Shade-intolerant seedlings established in high-intensity burn plots grew faster than those in all other treatments. Evidently, the increase in soil nutrients caused by high-intensity burns was not offset by altered soil structure. Importantly, the choice of tree species used as bioassays in these studies likely affected the results.

An important feature of the increase in resource availability produced by burns is the transient nature of the increases. Therefore, the first plants to become established after burns should benefit most from greater resource availability. Burns also greatly increased soil resource heterogeneity. Therefore, successful establishment and vigorous growth of plants after burns may be greatly influenced by chance, i.e., seeds dispersed into patches of well burned soil will exhibit higher growth than those dispersed into unburned soil or severely scorched soil.

CHAPTER 4
EFFECTS OF CANOPY GAP FORMATION, PLANT REMOVAL, AND
CONTROLLED BURNS OF HIGH AND LOW INTENSITIES ON
EARLY REGENERATION OF COMMERCIAL TREE SPECIES

Introduction

The most basic principle of sustainable forest management is that rates of timber harvesting should not exceed the rate at which timber volume accumulates (e.g., Johnson and Carbarle 1993, Dawkins and Philip 1998). This criterion requires sufficient regeneration of harvested species and, in many neotropical forests, poses the greatest barrier to sustainable forest management (e.g., Wyatt-Smith 1987, Verrisimo 1995, Gullison *et al.* 1996). There are several silvicultural means of improving poor regeneration, ranging from intensive techniques such as prescribed burning, to less intensive techniques such as selective harvesting without further treatment. Choice of technique must be knowledgeably based on the natural regeneration requirements of the target species. Presently, lack of information of the autoecology of many harvested tree species is one of the largest deterrents to sustainable timber production (Bazzaz 1990, Bazzaz and Pickett 1980, Fox 1976, Gomez-Pompa and Burley 1991, Hall 1996, Whitmore 1989).

For many decades, seedling ecology was a minor part of tropical forestry (Hall 1996); more recently, tropical seedling ecology has become the focus of much ecological research (e.g., Garwood 1983, Augspurger 1984a, 1984b, Swaine 1996, Kitajima 1996, Fenner and Kitajima 1998). The seedling stage is critical to regeneration as most mortality occurs early in the life of a tree (Lieberman 1996, Li *et al.* 1996). Understanding this life stage is also important for forest managers as species vary widely in their seedling ecology (Hall 1996), and the division of tree

72

species into regeneration guilds is based on seed germination and seedling establishment requirements. The most well defined group are species that require high light conditions for seed germination and seedling establishment and often colonize following disturbances (i.e., early-successional, Bazazz 1979; pioneer or secondary, Budowski 1965; or shade-intolerant, Swaine and Whitmore 1988). At the other end of the spectrum are species that can germinate and persist in the low light of forest understories (i.e., late-successional, Bazazz 1979; climax or primary, Budowski 1965; or shade-tolerant, Swaine and Whitmore 1988).

Tree species with different regeneration strategies require different silvicultural treatments to enhance their regeneration. For example, many shade-tolerant species have advanced regeneration in forest understories (Brokaw 1985b, Hartshorn 1989), therefore management techniques would mostly entail ensuring the survival of this regeneration during harvesting and enhancing its growth to mature stages. Enhancing regeneration of shade-intolerant species that do not have seedling banks in forest understories involves creating sites suitable for seed germination and seedling establishment and promoting safe arrival of seeds to these sites (Dickinson 1998).

In the seasonally dry forests of Bolivia, commercial tree species are represented in both shade-tolerant and shade-intolerant groups (Guzman 1997). Consequently, a mixed-management system was proposed for the community-owned forests of Lomerio (Pinard *et al.* 1999). Single-tree selection was recommended to enhance regeneration of shade-tolerant trees. Group selection, harvesting groups of trees to foster the development of even-aged patches, was suggested to improve regeneration of shade-intolerant species.

Prescribed burning of logging gaps has also been suggested as an additional treatment for the management of shade-intolerant species (Stanley 1995). Prescribed burns may enhance seedling establishment and growth of shade-intolerant species in a number of ways, including removing litter, reducing logging slash, and slowing vine proliferation (Stanley 1999). Abundant regeneration of shade-intolerant species after wildfire in Lomerio (Mostacedo *et al.* 1999, Gould *et*

al. 1999) lends further support to the promise of prescribed burns as a silvicultural tool for the management of dry forests in Bolivia.

Although the pioneer-climax dichotomy provides an often useful paradigm for ecologists, regeneration strategies of many tree species fall between the two extremes of completely shade-intolerant or shade-tolerant (Augspurger 1984b, Condit *et al.* 1996). In fact, most rain forest tree species are both shade-tolerant and gap-dependent, meaning they have the ability to persist in a seedling bank in forest understories but require canopy opening to reach maturity (Hartshorn 1989). And, as there is a continuum of species regeneration strategies, there is also a gradient of disturbance intensities among potential silvicultural treatments. The interaction of individual species' biology and silvicultural treatments of varying intensities is inherently complex. Before management techniques can be prescribed on a large scale, the effects of these techniques on all of the species in question need to be examined. For example, what are the effects of more intense disturbances, such as high-intensity fires, on the advance regeneration shade-tolerant trees? Or, what is the minimum disturbance level required for the regeneration of shade-intolerant trees?

In this chapter, I examine the range of responses of commercial timber tree species to experimental canopy opening, above-ground biomass removal, and controlled burns of high and low intensities and compare these responses to those in forest understories. My objective was to determine which gap treatment provided the best conditions for the establishment and growth of each species. I also address the question of whether regeneration of each of these species is limited by seed dispersal or by sites suitable for their establishment and growth. I approached these questions by studying the effects of gap treatments on seed germination, seed predation, vegetative regeneration, and seedling and sprout growth and mortality. Finally, I discuss results in relation to silvicultural management options for each species.

Methods

I conducted this study in the four gap treatments (high-intensity burn, low-intensity burn, plant removal, and gap control) applied to the 400 m^2 blocks described in Chapter 2. Trees were sampled in the paired 4 m^2 subplots positioned near the gap center and gap edge of each 100 m^2 treatment plot as well as the paired forest subplots (see Figure 2-4, Chapter 2).

Seed addition treatment

One randomly selected subplot (4 m^2) of each pair was assigned a seed addition treatment. Seeds of 5 commercial timber species were used in this treatment: *Anadenanthera colubrina, Astronium urundueva, Centrolobium microchate, Copaifera chodatiana,* and *Schinopsis brasiliensis* (hereafter referred to by genera; Table 4-1). I chose these species based on their commercial importance and seed availability in 1997. Seeds of all species were collected in the '95 coupe of Las Trancas from the forest floor and stored in cloth bags under a shelter until sown in plots. I removed all seeds that appeared to be damaged by predators or fungi. Twenty seeds each (= 5 seeds/m^2) of *Anadenanthera, Astronium,* and *Copaifera,* and 10 seeds each (= 2.5 seeds/m^2) of *Centrolobium* and *Schinopsis* were placed in each plot on the litter or soil surface, depending on the soil surface conditions in each treatment (Chapter 2).

Viability of collected seeds

Viability of seeds collected for the seed addition treatment was determined in germination trials conducted over a 60 day period (November-January) in Santa Cruz. One-hundred seeds of each of the 5 species were planted in 5 trays (20 seeds per tray) of a 50:50 mix of sand and soil. Trays were placed in a location receiving morning shade and afternoon sun and were watered each morning. Newly germinated seeds were counted and removed daily.

Table 4-1. Characteristics of tree species used in seed addition treatment or those species with sufficient regeneration for statistical analysis. All but *Acosmium* are commercial timber species. Ecological classifiaction of shade tolerance of regeneration taken from Pinard *et al.* 1998.

Species name	Family	Shade tol.	Dispersal	Dispersal unit	Fruit characteristics	Seed size
Acosmium cardenasii	Papilinoideae	3	wind	seed	legume,	10 x 15 mm, 1 mm thick
Anadenanthera colubrina	Mimosoideae	1	gravity	seed	legume, 10-25 cm long	12 x 10 mm, 1 mm thick
Aspidosperma rigidum	Apocynaceae	3	wind	seed	pod, 6 x 5 cm	25 x 20 mm, 1 mm thick
Astronium urundeuva	Anacardiaceae	1	wind	fruit	small dried drupe, calyx to 1 cm	3 mm diam.
Caesalpinia pluviosa	Caesalpinaceae	2	gravity	seed	legume, 10-15 cm long	10 x 10 mm 2-3 mm thick
Centrolobium microcheate	Papilinoideae	1	wind	fruit	samara, 8-10 cm long x 3-4 cm wide	12 x 2 mm
Copaifera chodatiana	Caesalpinaceae	3	animal	seed	dry pod, 2 x 3 cm seeds with oily aril	10 x 5 mm, 4 mm thick
Schinopsis brasiliensis	Anacardiaceae	1	wind	fruit	samara, 15-20 mm long x 5 mm wide	10 x 3 mm

Shade tolerance: 1 = shade intolerant; 2 = partially shade-tolerant; 3 = shade-tolerant

Density, height, and relative height growth rate measurements

Seedlings have been variously defined as individuals still dependent on seed reserves (e.g., Garwood 1996), to individuals up to 2.7 m tall (Whitmore 1996). In this study, I did not use size or physiology as a defining character, rather I define seedlings as individuals originating from seed as opposed to those regenerating as sprouts. I measured seedling and/or sprout density and height in each 4 m^2 subplot (both seeded and unseeded) at 1.5, 3, 6, 9, 12, and 18 months after burns. At each sampling period, all commercial species within subplots (of both seeded and unseeded species) were identified as sprouts or seedlings, tagged, and height to the apical meristem measured. Sprouts originating from the stem or root collar were easily identified because scars were visible. Root sprouts (root suckers) were more difficult to identify but were recognizable because the first leaves generally differed from the first true leaves of seedlings. Relative height growth rates (hereafter referred to as RGR) was calculated as:

$$RGR = [\ln (\text{height}_{t2}) - \ln (\text{height}_{t1})] / (t_2 - t_1)$$

where t_1 and t_2 are two measurement periods. Seedlings of *Anadenanthera* were extremely abundant in 1997, therefore a maximum of 3 randomly selected individuals per subplot were tagged for height measurements and the remaining individuals counted. Additionally, a maximum of 3 randomly selected individuals of *Acosmium cardenasii* were tagged in each plot and the remaining individuals counted. Although *Acosmium* is not commercially valuable due to its susceptibility to heart rot, I included it because it has the most abundant tree regeneration of any canopy tree species in Las Trancas '95. Many of the *Anadenanthera* seedlings had been browsed between the 6 and 9 month assessments, therefore I noted presence or absence of browsing of tagged individuals.

Statistics analyses

Seedling densities of most tree species could not be normalized, therefore seedling densities were analyzed using Kruskall-Wallis non-parametric tests (SPSS 1997). Separate tests were run for each species by month, testing for the effects of the seeding treatment and gap treatments on densities. For species that regenerated from both seeds and sprouts, these regeneration modes were analyzed separately. Square-root transformed densities of *Acosmium* and *Anadenanthera* were normally distributed, therefore densities of these species were compared using repeated measures ANOVAs. For *Anadenanthera*, the seeding treatment and gap treatments were factors in the ANOVA model. For *Acosmium*, gap treatments and regeneration mode were used as factors, as this species was not used in the seeding treatment but regenerated from both seeds and sprouts.

Seedling height and RGR were analyzed separately for each species using repeated measures ANOVAs with gap treatments and, for the species that sprouted, regeneration mode as factors. The effects of location within gap on seedling height and RGR was tested for *Anadenanthera*; other species were not sufficiently abundant for this test. Also, the effect of treatment on proportion of *Anadenanthera* seedlings browsed was tested with an ANOVA. Blocks were random effects in each of the above models.

Effects of treatments on seed predation

A seed predation study was conducted to compare rates of seed predation among treatments and at varying distances from gap centers. Two species were chosen for this study: *Centrolobium* and *Copaifera*. In each treatment, 2 seeds of each species were placed at each of five stations 1, 3, 5, 7, and 9 m from the gap center. Seeds were inspected after 2 and 9 weeks for removal or signs of predation. In this study, I assumed that removal indicated predation and therefore use "predation" as the sum of removed seeds and damaged seeds. The effects of treatment and distance from gap center on seed predation were tested using Kruskal-Wallis tests on proportions of seeds remaining and undamaged after 9 weeks.

Effects of the low-intensity burn treatment on seed germination

To assess the effect of low-intensity burns on seed germination of 3 commercial tree species, 5 seeds each of *Copaifera chodatiana*, *Centrolobium microchaete*, and *Schinopsis brasiliensis* were placed on leaf litter in low-burn plots just prior to controlled burns. After burns, remaining seeds were retrieved and transported to the nearby community of San Lorenzo for germination trials. Seeds from burned plots were placed in plastic trays with sand and watered daily for 2 months. To detect if germination was related to degree of burn damage, seeds were inspected before germination trials and assigned a damage score. Seeds of *Centrolobium* and *Schinopsis,* which are protected by a dry husk, had 6 damage categories relating to the degree of damage to the fruit: 0 (no damage) to 5 (fruit completely burned). *Copaifera,* which is dispersed with only a fleshy aril, had 3 damage categories relating to the degree of visible damage to the seed. The percentage of seeds germinating within each damage category were compared using a Chi-squared test for independence.

Results

Seed viability of species used in seed addition treatment

Seeds of *Copaifera* demonstrated the highest viability in greenhouse germination trials, followed by *Anadenanthera*, *Astronium*, *Schinopsis*, and *Centrolobium* (Figure 4-1). Seeds of *Anadenanthera* and *Astronium* germinated most rapidly; of their viable seed, 80% and 83%, respectively, germinated within 4 days.

Effects of treatments on seed predation

Seed predation was uncommon in gaps and there were no differences among treatments (*Copaifera* P = 1.00; *Centrolobium* P = 0.30) or distance from gap edge (*Copaifera* P = 0.91; *Centrolobium* P = 0.73). Overall, 17% of *Copaifera* and 5% of *Centrolobium* seeds were removed or had evidence of predation over the 9 week observation period.
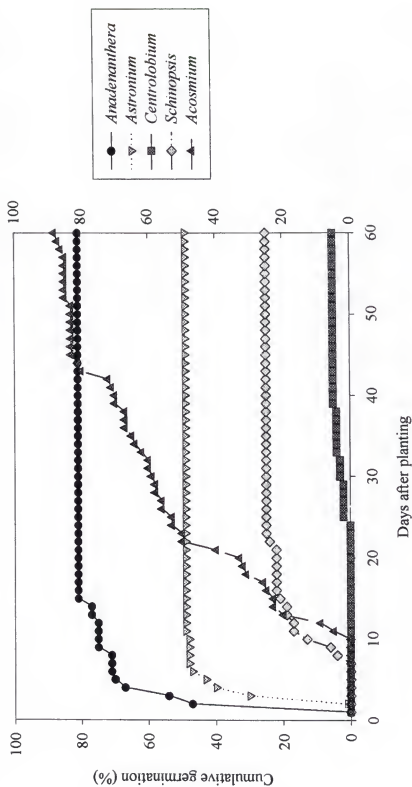
Figure 4-1. Greenhouse seed germination trial of the 5 commercial tree species used in the seeding treatment. Results represent the cumulative percentages of 100 seeds germinated each day over a 60 day germination trial.

Effects of low-intensity burns on seed germination

Low-intensity burns either decreased or did not affect seed germination of *Copaifera*, *Centrolobium*, and *Schinopsis*. *Copaifera* seeds placed in low-intensity burns had an overall germination rate of 35%, less than half the germination rate of seeds used in the seed viability germination trial (88%). Percent germination of *Copaifera* seeds was dependent on the degree of burn damage ($X^2 = 9.5$, $P < 0.05$). Germination rates of *Schinopsis* seeds placed in low-intensity burns were also lower than unburned seeds (4% compared with 26%), however numbers were too low for analysis. *Centrolobium* seeds placed in low-intensity burn plots had germination rates of 4%, only slightly lower than the germination of unburned seeds (5%).

Treatment effects on seedling densities of commercial tree species

Effects of seed addition treatment. Seed addition significantly increased seedling densities of *Centrolobium* and *Copaifera* but not those of *Anadenanthera* or *Astronium* (Tables 4-2, 4-3). Only 9 individuals of *Schinopsis* were recorded in all subplots; of these individuals, 6 were in seeded plots.

Effects of gap treatments. Patterns of commercial tree density among treatments and over the 18 month sampling period varied among species. For simplicity, I have displayed commercial species that had similar density patterns over the 18 months together as groups in Figure 4-2. Significant differences among treatments are reported separately for each species in Tables 4-3 and 4-4 and treated in more detail in following sections.

Density of the first group (*Anadenanthera* and *Astronium*), all true seedlings, peaked within 3 months after burns and declined thereafter. Density of the second group (*Copaifera*, *Aspidosperma*, and *Caesalpinia*) differed according to regeneration mode. While seedling density of this group gradually increased throughout the 18 month observation period, sprout density remained fairly constant after the first 3 months. The third group consists of one species (*Centrolobium*) that regenerated predominately as root sprouts. Seedlings of *Centrolobium*, which

Table 4-2. Summary of seed fall and seedling densities of 7 commercial tree species and a non-commercial tree species (*Acosmium cardenasii*). Seed fall refers to seedfall before or after the prescribed burn treatments (August 30-September 2, 1997). Significance values for the seeding treatment are only given for seeded species. Due to the delayed germination of several species, the effects of the seeding treatment was not detected until 12 months following treatments. For these species, densities and significance values are reported for 12 months. For species not used in the seeding treatment, total density (seedlings and sprouts combined) at the end of the study (18 months) is reported with the exception of the 1st year cohort of *Caesalpinia*, and *Acosmium*, whose densities are reported for 12 months. Pre-treatment density is based on a pre-logging inventory conducted in 1995 in the same logging coupe before logging activities (Killeen *et al.* 1998).

Species	Seed fall before or after burns	Seed addition density of added seeds (m^{-2})	Seedling density unseeded density (m^{-2})	seeded density (m^{-2})	Months following treatment	Sig. of seeding treatment	Pre-treatment density (m^{-2})
Seeded species							
Anadenanthera	both	5	1.9	2.7	3	NS	0.05[b]
Astronium	after	5	0.05	0.09	3	NS	0.002
Centrolobium	before	2.5	0	0.04	12	***	0
Copaifera	before	5	0.04	0.16	12	***	0.15
Schinopsis	both	2.5	0.003	0.009	12	N/A[a]	0
unseeded species							
Caesalpinia (1st year cohort)	before		0.03	-	12	-	0.025
Caesalpinia (2nd year cohort)	after		0.06	-	18	-	
Aspidosperma	after		0.05	-	18	-	0.08
Acosmium	after		0.6	-	12	-	0.71

*** P < 0.001, ** 0.001 < P < 0.01, * 0.01 < P < 0.05, NS = not significant

[a] Numbers too low for statistical analysis, justification described in text.

[b] Likely seedlings germinated in 1995, the year of the census, as no seedlings of these species > 1-yr old were found in forest plots in this study.

Table 4-3. Statistical analyses testing for the effect of the seed addition treatment. Seedling densities of *Astronium, Centrolobium*, and *Copaifera* could not be normalized, therefore the effects of the seeding treatment was tested with a Kruskall Wallis non-parametric test for each month. Square root transformed seedling densities of *Anadenanthera* were normally distributed, therefore a repeated measures ANOVA was used to test the effect of the seeding treatment and gap treatments for this species. Because a significant time*treatment interaction was found for *Anadenanthera* an ANOVA was used to analyze each month separately.

Month	*Astronium*		*Copaifera*		*Centrolobium*	
	X^2	P	X^2	P	X^2	P
3	0.9	0.34	1.1	0.29	1.0	0.32
6	1.3	0.25	13.4	0.00	6.2	0.01
9	0.7	0.40	20.0	0.00	15.2	0.00
12	1.0	0.31	26.0	0.00	15.2	0.00
18	0.7	0.40	23.7	0.00	3.0	0.08

	Anadenanthera			
	seeding treatment		gap treatments	
Month	F	P	F	P
3	3.4	0.07	6.1	0.000
6	3.5	0.06	2.9	0.03
9	3.3	0.07	2.8	0.03
12	2.7	0.10	3.8	0.01
18	1.8	0.17	5.1	0.001
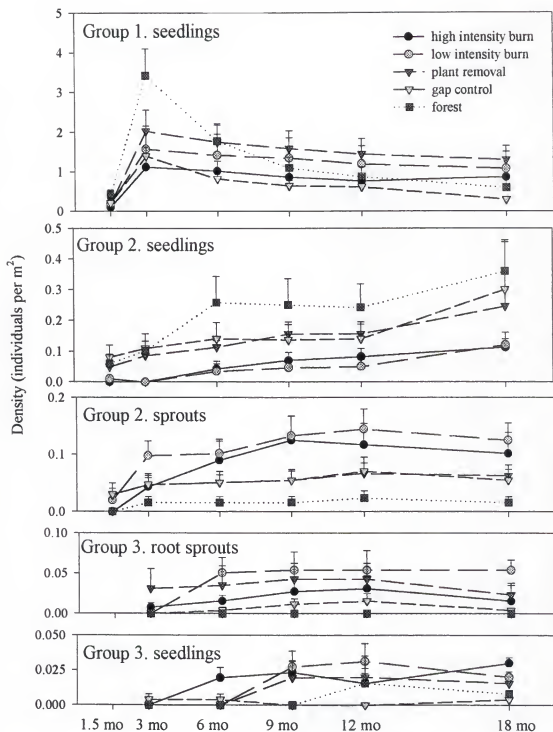
Figure 4-2. Densities of commercial species over the 18 month sampling period following experimental burns. Species are grouped according to similar regeneration strategies. Group 1 (*Anadenanthera* and *Astronium*) were found predominately as seedlings, Group 2 (*Aspidosperma*, *Copaifera*, and *Caesalpinia*) were found as both seedlings and sprouts, and Group 3 (*Centrolobium*) was found predominately as root sprouts (bars = S.E.; n = 16).

were rare, established slowly over the first year and many died by 18 months. In contrast, density of *Centrolobium* root sprouts remained relatively constant throughout the sampling period.

The prolonged seedling establishment and sprouting of species in these last 2 groups restricted the calculations of RGR to the later part of the 18 month sampling period. For these species, I calculated RGRs from no earlier than 6 or 9 months due to the low seedling and sprout densities at 3 months. This method of calculating RGR may have limited detection of treatment differences. If the most rapid growth occurs during the first several weeks following germination or sprouting, then differences in RGRs measured after this initial growth spurt may not be detectable. For this reason, seemingly contradictory results were obtained for some species in the following results sections (i.e., *Aspidosperma* and *Copaifera*), where seedling heights were significantly different among treatments whereas RGRs were not.

Treatment effects on seedling densities, heights, RGRs, and survival of seeded species

Anadenanthera. Seedlings of *Anadenanthera* were the most abundant of all commercial tree species with an average density throughout the treatments of 1.1 ± 0.4 seedlings/m^2 (mean $\pm$ 1 S.E.) 18 months following treatments. All *Anadenanthera* seedlings in these analyses are from the 1997 cohort. Seed production of *Anadenanthera* in 1997 was larger than most years according to locals. I did not encounter any seedlings > 1 yr-old in subplots, and due to extremely low seed production in 1998, I also did not encounter *Anadenanthera* seedlings germinating in 1998. Although *Anadenanthera* has the ability to coppice (pers. obs.), I did not encounter any sprouts in the 4 m^2 subplots.

Three months after burns, *Anadenanthera* seedling density was highest in forest plots (F = 6.1, P < 0.001; Figure 4-3). Density declined in forest plots due to high mortality and by 12 months, seedling densities were highest in the plant removal treatment (F = 3.8, P = 0.02). *Anadenanthera* seedling density was lowest in gap controls throughout the study.
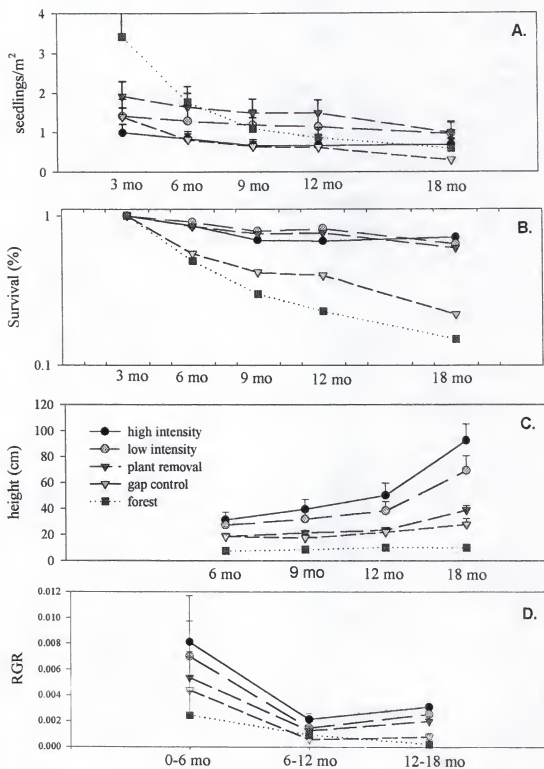
Figure 4-3. A. Seedling density, B. percent seedling survival, C. seedling height, and D. seedling relative height growth rates for *Anadenanthera colubrina* in the four gap treatments and forest plot. All graphs follow the legend shown in graph C (bars = S E.; n = 16).

Height of *Anadenanthera* seedlings averaged 49 ± 5 cm after 18 months. The tallest seedling measured was 3 m and was found in a high-intensity burn plot. Seedlings in high and low-intensity burn treatments were significantly taller than seedlings in the gap control or forest understory; seedling height in the plant removal treatment was intermediate ($F = 15.4$, $P < 0.001$). Correspondingly, differences in RGRs among treatments were significant and patterns followed those for height ($F = 18.4$, $P < 0.001$). *Anadenanthera* seedlings were taller and had higher RGRs in gap centers than near gap edges ($F = 21.8$, $P = < 0.001$; $F = 16.0$, $P = < 0.001$). After 18 months, seedlings in gap centers averaged 25 cm taller than seedlings near gap edges.

A mean of 21% (at 9 months) and 12% (at 12 months) of *Anadenanthera* seedlings were browsed (tracks suggest by brocket deer, *Mazama* sp.). Seedlings in high-intensity burn treatments suffered the highest rates of browsing while seedlings in the forest experienced the lowest rates ($F = 11.16$, $P < 0.001$).

Astronium. Pattern of *Astronium* seedling density was strongly related to disturbance intensity (Table 4-4). Throughout the 18 month sampling period, the highest seedling densities were found in the high-intensity burn treatment plots followed by the low-intensity burn and plant removal treatments (Figure 4-4). Mortality rates in these treatments was moderately high. Only 2 *Astronium* individuals were found in all 16 gap control plots (but these died during the 18 month sampling period) and no *Astronium* seedlings were found in forest plots. I encountered only one sprout of *Astronium* in the permanent subplots (a low-intensity burn treatment) and did not include it in these analyses.

Height of *Astronium* seedlings averaged 110 ± 14 cm after 18 months, the tallest mean seedling height among species. Although heights and RGRs of *Astronium* seedlings were not significantly different among treatments ($F = 4.0$, $P = 0.11$; $F = 1.0$, $P = 0.40$, respectively), there was a distinct trend of taller *Astronium* seedlings with increasing disturbance intensity. Mean
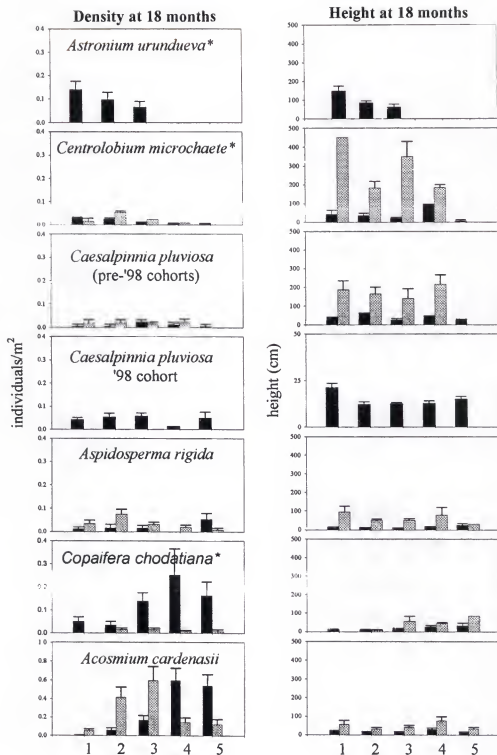
Figure 4-4. Densities and heights of seedlings (black bars) and sprouts (grey bars) of 6 species 18 months following treatments (* = seeded species). Treatment codes along the x-axis are: 1= high intensity burn, 2 = low intensity burn, 3 = plant removal, 4 = gap control, 5 = forest (bars = S.E.; n = 16).

Table 4-4. Statistical analyses testing for differences among gap treatments and forest understory plots. Seedling densities of *Astronium*, *Aspidosperma*, *Caesalpinia*, *Centrolobium*, and *Copaifera* could not be normalized, therefore the effect of gap treatments was tested using a Kruskall Wallis non-parametric test for each month. Seedlings and sprouts were also analyzed separately for these species (if applicable). Square-root transformed densities of *Acosmium* were normally distributed, therefore a repeated measures ANOVA was used to test of the effect of the gap treatments and regeneration mode (seedling or sprout) for this species. A significant regeneration mode*treatment was found, therefore seedlings and sprouts were then analyzed separately.

| | Astronium | | Aspidosperma | | | | Caesalpinia | | | | Centrolobium | | | | Copaifera | | | |
| | seedlings only | | seedlings | | sprouts | | seedlings | | sprouts | | seedlings | | root suckers | | seedlings | | sprouts | |
Mo	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p
3	25.1	<0.001	9.9	0.04	7.7	0.10	21.2	0	8.6	0.07	4.0	0.41	11.1	0.03	17.5	0.002	6.2	0.18
6	34.7	<0.001	9.9	0.04	6.7	0.16	14.6	0.006	8.6	0.07	16.2	0.003	11.2	0.02	12.8	0.01	6.2	0.18
9	37.6	<0.001	4.0	0.40	12.1	0.02	11.6	0.021	6.8	0.15	11.8	0.02	23.2	<0.001	12.3	0.02	5.2	0.26
12	37.0	<0.001	5.5	0.24	12.0	0.02	11.6	0.021	5.6	0.23	5.6	0.24	18.5	0.001	10.4	0.03	6.1	0.19
18	37.5	<0.001	7.5	0.11	12.1	0.02	4.3	0.37	5.6	0.23	2.0	0.73	21.6	<0.001	11.5	0.02	6.1	0.20

| Acosmium | | | |
Source of variation	df	F	P
Block	15	2.2	0.01
Regeneration mode	1	0.0	0.93
Treatment	4	3.6	0.01
Mode * Treatment	4	4.0	0.01
Error	65		

| Acosmium | | seedlings | | sprouts | |
Source of variation	df	F	P	F	P
Block	1	1.1	0.40	1.2	0.29
Treatment	15	12.1	<.001	11.3	<.001
Error	4				

height of *Astronium* seedlings in high-intensity burn treatments was 150 cm, more than twice the height of seedlings in plant removal treatments (65 cm). Also, the tallest *Astronium* seedling (4 m) was found in a high-intensity burn plot.

    Copaifera. *Copaifera* regenerated from both seeds and sprouts, although the overall density of seedlings was more than 10 times higher than sprouts (Table 4-5). *Copaifera* seedlings were most abundant in gap control plots; sprout density did not differ among treatments (Table 4-4, Figure 4-4). Mortality was low throughout the study period, particularly for sprouts (Table 4-6).

    Sprouts of *Copaifera* were taller than seedlings (F = 8.4, P = 0.01), although their RGRs did not differ (F = 1.8, P = 0.20). Height and RGRs did not differ among treatments (F = 0.3, P = 0.47; F = 0.3, P = 0.84, respectively).

    Centrolobium. *Centrolobium* regenerated both from seeds and root sprouts. Density of root sprouts was higher than seedling density at 6 months (Table 4-5). Apparently none of the seedlings arose from naturally dispersed seeds; natural regeneration of this species was composed entirely of root sprouts. At 3 months, *Centrolobium* root sprouts were most abundant in the plant removal treatment; from 6 to 18 months they were most abundant in the low-intensity burn treatment (Table 4-4, Figure 4-2). At 6 months, *Centrolobium* seedlings were most abundant in the high-intensity burn treatment; at 9 months they were most abundant in the burned and plant removal treatments. Seedling mortality was greater than root sprout mortality (Table 4-6).

    Centrolobium sprouts averaged 267 cm tall after 18 months, more than 7 times the mean height of *Centrolobium* seedlings (37 cm; F = 39.2, P = 0.003; Figure 4-4). Similarly, RGRs of *Centrolobium* sprouts were also higher than those of seedlings (F = 13.6, P = 0.01). No differences in heights at 18 months or RGRs were detected among treatments (F = 1.0, P = 0.49; F = 0.1, P = 0.97, respectively).

    Schinopsis brasilensis. A total of 9 *Schinopsis* seedlings were recorded in all subplots, although the maximum number at any one sampling period was 7 (Table 4-7). After 18 months, 6

Table 4-5. Statistical analyses comparing seedling and sprout densities of *Aspidosperma*, *Caesalpinia*, *Centrolobium*, and *Copaifera*. Seedling and sprout densities of these species could not be normalized, therefore a Kruskall-Wallis non-parametric test was used to analyze each month.

Month	*Copaifera* X^2	P	*Centrolobium* X^2	P	*Aspidosperma* X^2	P	*Caesalpinnia* X^2	P
3	5.6	0.02	3.7	0.06	7.7	0.006	0.13	0.72
6	22.2	0.00	5.9	0.02	11.2	0.001	0.32	0.57
9	27.6	0.00	2.6	0.11	10.2	0.001	0.04	0.84
12	31.5	0.00	2.2	0.13	15.2	0.000	0.001	0.98
18	35.9	0.00	3.1	0.08	10.2	0.001	15.6	0.00

Table 4-6. Killing power, a parameter similar to mortality rate, for 5 commercial tree species in the four gap treatments and forest understory plots. Killing power (k) is calculated separately for seedlings and sprouts of each species, except for *Astronium*, for which no sprouts were found. Killing power is calculated as $(\log_{10}a_x - \log_{10}a_{x+1})$, where a_x represents the number of individuals in the first cohort following treatments, and a_{x+1} is the number of these individuals surviving into the next year (Begon and Mortimer 1981). The numbers of individuals that died during this period are listed in columns "#."

Species		high intensity burn k	#	low intensity burn k	#	plant removal k	#	gap control k	#	forest k	#	All individuals k	#
Aspidosperma	seedlings	0.20	3	0.30	1	0.30	1	0.60	3	0.15	2	0.25	10
	resprouts	0.00	0	0.22	9	0.05	1	0.48	4	*	1	0.17	15
Caesalpinia	seedlings	0.00	0	0.00	0	0.07	1	0.22	2	0.00	0	0.09	3
	resprouts	0.00	0	0.11	2	0.00	0	0.06	1			0.05	3
Centrolobium	seedlings	0.11	2	0.12	4	0.06	1	*	1	*	2	0.14	10
	resprouts	0.18	1	0.00	0	0.11	2	0.12	1			0.07	5
Copaifera	seedlings	0.09	3	0.10	2	0.09	6	0.06	4	0.13	5	0.09	20
	resprouts	0.00	0	0.00	0	0.08	1	0.00	0	0.00	0	0.02	1
Astronium	seedlings	0.11	10	0.13	9	0.18	9	*	1			0.14	29

* = where a_{x+1} was equal to 0 (all individuals died), k equals infinity

seedlings remained for an overall density of 0.005 seedlings/m². With such a small sample it is difficult to determine if seed addition significantly increased seedling density. Although the majority of seedlings were in seeded plots (6 of the total 9), distribution among gaps was distinctly clumped with all 9 seedlings found in only 4 gaps, and 4 seedlings in a gap with a mature *Schinopsis* nearby. These observations suggest that most of the seedlings established from naturally dispersed seeds. Although *Schinopsis* was not statistically analyzed due to its small sample size, it appears to favor establishment in burned areas. Of the 9 seedlings, 55% were in high-intensity burn plots, 25% in low-intensity burn plots, and one seedling each in a plant removal treatment and forest plot (although both of these seedlings died). Average height of *Schinopsis* seedlings surviving at 18 months was 43 cm.

Treatment effects on seedling densities, heights, RGRs, and survival of non-seeded species

      Acosmium cardenasii. *Acosmium* was the second most abundant species with an average density of 0.6 individuals/m² 18 months following treatments. Roughly half (57%) of *Acosmium* individuals were sprouts (Table 4-4). Patterns of seedling and sprout densities among treatments differed. Seedling densities showed a negative response to disturbance intensity (Figure 4-4). The lowest seedling densities were found in high-intensity burn treatments while the highest densities were in gap control and forest plots. In contrast, sprout density was highest in the plant removal and low-intensity burn treatments.

      There were no differences among seedlings and sprouts in height or RGR (F = 2.7, P = 0.11; F = 0.7, P = 0.42, respectively) although heights and RGRs of both seedlings and sprouts differed slightly among treatments. Both seedlings and sprouts were tallest in gap controls (F = 4.8, P = 0.01), a pattern that likely resulted because individuals already established in these plots prior to gap formation were cut to a height of 2 m in the gap control, whereas in the other treatments they were cut to soil level or burned. Actual RGR was higher in high and low-intensity burn treatments than gap controls (F = 6.0, P = 0.002).

Caesalpinia pluviosa. *Caesalpinia* had abundant seed rain the second year of the study (1998). Approximately 0.06 new seedlings/m^2 were added to the existing seedling bank of 0.03 seedlings/m^2. *Caesalpinia* regenerated from both seeds and sprouts, and before the abundant seed fall in '98, seedlings and sprouts occurred with roughly equal frequency (0.015 seedlings vs. 0.016 sprouts/m^2). After the seed rain in 1998, seedlings were 3 times more common than sprouts (Table 4-5). Excluding the 98' cohort, *Caesalpinia* seedlings were most abundant in forest plots; there was no difference in sprout density among treatments (Table 4-4, Figure 4-4). Among seedlings of the '98 cohort, there were no differences in density among treatments. Mortality was low throughout the study period for both seedlings and sprouts (Table 4-6).

Caesalpinia sprouts were taller than seedlings (F = 9.3, P = 0.01), although RGRs did not differ (F = 0.2, P = 0.66). There were no treatment differences in heights or RGRs among individuals in the pre-'98 cohort (F = 0.1, P = 0.95; F = 0.6, P = 0.63, respectively) or among seedlings in the '98 cohort (F = 1.0, P = 0.44; F = 1.0, P = 0.44, respectively).

Aspidosperma rigidum. *Aspidosperma* sprouts were more abundant than seedlings (Table 4-5). Differences in seedling density among treatments were only found at 3 and 6 months; at these sampling periods, seedlings were most abundant in the forest understory (Table 4-4, Figure 4-4). Sprout density was most abundant in the low-intensity burn treatment after 9, 12, and 18 months. Mortality of both seedlings and sprouts was moderate (Table 4-6).

Aspidosperma sprouts were taller than seedlings (F = 14.8, P = 0.003). RGRs among sprouts and seedlings did not differ (F = 0.01, P = 0.84). There was no pattern in height or RGRs among treatments (F = 3.4, P = 0.07; F = 1.3, P = 0.32).

Additional commercial tree species found at low densities. Four additional commercial species were found at very low densities in treatment subplots: *Cordia alliodora, Phyllostylon rhamnoides, Pithecellobium* sp., and *Platymiscium uleii* (Table 4-7). Combined density of these species and *Schinopsis*, a seeded species, was highest in high-intensity burn subplots, followed by

Table 4-7. Densities and heights of commercial tree species found in the four gap treatments and forest understory plots at low frequencies. Total number is the number of individuals in all treatments at 18 months following treatments. Percent sprouting is based on the total number of individuals. Densities and heights within treatments represents values 18 months following treatments.

			Treatments									
			High intensity		Low intensity		Plant removal		Gap control		Forest	
Species	Total number	Percent sprouting	density (#/m²)	height (cm)	density (#/m²)	height (cm)	density (#/m²)	height (cm)	density (#/m²)	height (cm)	density (#/m²)	height (cm)
seeded species												
Schinopsis brasiliensis	6	0%	0.020	45	0.004	35	0		0		0	
unseeded species												
Cordia alliodora	1	100%	0.004	190	0		0		0		0	
Phyllostylon rhamniodes	3	0%	0.008	18	0.004	5	0		0		0	
Pithecellobium sp.	4	50%	0.004	25	0.008	65	0.004	135	0		0	
Platymiscium ulei	7	100%	0.004	110	0.012	163	0.012	210	0		0	
Averages per treatment			0.005	86	0.006	67	0.004	135	0		0	

low-intensity burn and plant removal subplots. None of these species were found in gap control or forest subplots.

Discussion

Effects of treatments on seed predation

The rates of seed predation of *Copaifera* (17%) and *Centrolobium* (5%) observed in this study are much lower than those reported in the literature. Crawley (1992) found that post-dispersal seed predation reviewed over a variety of ecotypes averaged 45-50% and often approached 100%. Among studies conducted in tropical forests, reported rates of seed predation are even higher (36-98% DeSteven and Putz 1984; 50-90% Schupp 1988; 27-98% Alvarez-Buyella and Martinez-Ramos 1990; 25-94% Hammond 1995; 20-100% Holl and Ludlow 1997).

The low seed predation found for these 2 species in this study may have been due to several factors. Seeds removed from areas of high seed density near parent trees and placed beyond the typical range of seed dispersal may escape predation by specialists (Janzen 1970, Connell 1971, but see Augspurger and Kitajima 1992). Both *Copaifera* and *Centrolobium* appeared to suffer high rates of seed predation on or near parent trees. Fredericksen et al. (2000) reported that 34% of *Copaifera* and 41% of *Centrolobium* seeds beneath parent trees were damaged. Curculionid beetles and rodents were observed eating *Copaifera* seeds, and *Cebus* monkeys, parrots, and squirrels were observed eating *Centrolobium* seeds (Fredericksen *et al.* 2000). *Centrolobium* also suffered high rates of pre-dispersal predation: of a sample of 110 recently dispersed fruits, 28% had either exit holes or larvae inside (pers. obs.).

The low rates of seed predation observed in this study may also be due to the fact that only the gap control treatment offered any protection for potential seed predators. Most woody debris was removed or burned in the other three treatments, and colonizing vegetation was not thick until a few months after seeds were placed out. Schupp *et al.* (1989) found that seed predation was

higher in disturbed areas than forest understories due to the number of small rodents that take refuge in brush.

I found no effect of distance from forest edge on seed predation, a result which agrees with those of Holl and Ludlow (1997). Overall, these low predation rates suggest that seed predation had little effect on seed densities of *Copaifera* and *Centrolobium* after their dispersal or placement in gap treatments. However, seed predation may have been important for other species or during other seasons. For example, in a different experiment (Chapter 3) more than half of 720 *Anadenanthera* seeds were damaged or removed, primarily by leaf cutter ants (*Atta* sp.). This occurred in November after the start of the rainy season, when seeds has imbibed water and were starting to germinate. In contrast, I did not observe any predation of *Anadenanthera* seeds that were placed out in October, before rains began.

Effects of controlled burns on seed germination of selected tree species

Decreased germination rates of seeds subjected to low-intensity burns indicates this treatment may have contributed to lower seedling densities for species with peak seed fall before burns (e.g., *Copaifera*, *Centrolobium*). Low seedling densities from seed banks sampled after low-intensity burns (Chapter 5) suggests most species in this forest have decreased germination after exposure to low-intensity fire. Extremely low seedling densities from seed banks sampled after high-intensity burns (Chapter 5) indicate that most burned seeds are killed during intense fires. Similar results were reported by Brinkmann and Vieira (1971) in their study of the effects of fire on regeneration from buried seeds in the Amazon rain forest. They found that seeds of 31 tropical tree species were killed during slash burning. These findings indicate that the timing of controlled burns relative to peak seed fall can alter amounts of viable seed, and therefore is an important factor in commercial seedling density.

Effects of seeding treatment on tree seedling densities

Seed addition increased seedling densities of 2 species (*Centrolobium* and *Copaifera*,) but did not affect seedling densities in the remaining 3 (*Anadenanthera*, *Astronium* and *Schinopsis*). Increased seedling densities following seed addition indicates that seeds are limiting, either because seed production is low or because seeds fail to reach all sites suitable for their germination and establishment (i.e., dispersal limitation; Dalling 1998). Both *Copaifera* and *Centrolobium* produced abundant seed in 1997 (Fredericksen *et al.* 2000), so it is unlikely that seed production was limiting during the year of this study. Both species show characteristics of dispersal limitation, due to either their dispersal mode or the distribution of mature trees. For example, *Copaifera* seeds mostly fall beneath the parent tree or may be carried short distances by ants or small mammals (Fredericksen and Justiniano 1998). Only 4 of 16 gaps had mature *Copaifera* within 15 m of the gap edge, so it is likely that naturally dispersed seeds were scarce in the remaining 12 gaps. *Centrolobium* produces large samaras, fruits that can easily reach gap centers aided by the strong winds of the dry season (Chapter 5). However, only 9 of the 16 gaps had mature *Centrolobium* trees within 15 m of the gap edge, so it is likely seeds of this species were scarce in the remaining 7 gaps.

The timing of seed dispersal relative to burns also may have contributed to the significant effect of the seed addition treatment for *Copaifera* and *Centrolobium*. Seed fall of both species occurred before controlled burns. Naturally dispersed seeds present in plots before burns were likely damaged or killed, which would contribute to higher seedling densities in seeded plots of the burned treatments.

Astronium and *Schinopsis* seedling densities were apparently not increased by seed addition. Seedling densities of *Astronium* and *Schinopsis* were highest in the intensely burned treatments and absent from forest and control plots. This pattern suggests that, for these 2 species, seedling recruitment is limited more by the availability of sites suitable for germination and

establishment (establishment limitation; Dalling 1998) than by seed production or dispersal. Although it is unclear from this study, it can be argued that higher *Astronium* and *Schinopsis* seedling densities in the intensely disturbed treatments were due more to higher seedling survival than to enhanced seed germination. Although intense disturbances produce several effects which have been shown to promote seed germination of some species, including litter removal (Vazquez-Yanes *et al.* 1990), soil exposure (Putz 1983), increased light (Vazquez-Yanes and Smith 1982), and increased soil temperature (Probert 1992, Cervantes 1996), regulation of germination by these cues are more characteristic of a specialized group of short-lived pioneer species such as *Cecropia* spp. Seeds of most tropical tree species lack a period of dormancy (Vazquez-Yanes and Orozco Segovia 1993, Garwood 1989); those that exhibit dormancy usually germinate in response to increased moisture (Vazquez-Yanes and Orozco-Segovia 1993), particularly in seasonal forests (Garwood 1983). It is likely that seeds of *Astronium* and *Schinopsis* germinated but quickly died and were missed in the first census. Seedling mortality is reported to be higher in forest understorys than gaps (Veenendall *et al.* 1995), particularly for shade-intolerant species (Kitajima 1994, Li *et al.* 1996), and the greatest mortality due to unsuitable habitat conditions occurs very early in the life of seedlings (Li *et al.* 1996).

In contrast to the other 4 seeded species, *Anadenanthera* recruitment does not appear to be limited by seed production, seed dispersal, or suitable germination and establishment sites. As previously discussed, seed production of *Anadenanthera* was abundant in 1997. And, although *Anadenanthera* seeds are primarily gravity dispersed (Justiniano and Fredericksen 1998), all 16 gaps had at least one mature *Anadenanthera* within 15 m and seeds were dispersed into most gaps (Chapter 5). Also, seedling establishment does not appear to be controlled by microsite availability as *Anadenanthera* seedlings were present in all treatments. Although *Anadenanthera* seedling recruitment was abundant during the year of this study, it may be limited in other years. Taking into account the scarcity of seeds produced in 1998, *Anadenanthera*'s reproductive phenology fits

characteristics of a masting species (Kelly 1994). In non-masting years, seed production and subsequent seedling recruitment of masting species is low (Whitmore 1984). Therefore, for this species, synchrony of harvesting activities and silvicultural treatments with years of seed production is necessary to ensure sufficient regeneration; silvicultural treatments applied during years of low seed production will not result in abundant seedling recruitment. Timber species with irregular reproductive phenologies may complicate long-term management planning due to the difficulty of predicting masting years.

Gap treatment effects on tree regeneration

Regeneration strategies. Gap treatments had significant effects on the regeneration of all of the tree species studied, but each species responded differently to the treatments. While seedling density and height of some species varied among treatments, the mode of regeneration (from seeds or sprouts) of other species was more affected. The response of these tree species to the treatments highlights their unique regeneration strategies; no single pattern neatly describes the whole. However, I will attempt to generalize the responses according to the predominate regeneration mode of the species (from seeds, sprouts, or both).

Based on regeneration mode, three patterns of species response to treatments can be identified: species that regenerated primarily from seed (*Anadenanthera* and *Astronium*), species that regenerated from both seeds and sprouts (*Caesalpinia, Copaifera, Acosmium, Aspidosperma*), and species that regenerated by root sprouting or suckering (*Centrolobium*). These groups correspond to groups 1, 2, and 3 in Figure 4-2 (*Acosmium* was not included in this graph because it is not commercially valuable). A summary of treatment effects on the density, height and RGRs of these groups is displayed in Table 4-8.

The response of these groups to treatments reflects their pre-gap seedling density, which is more-or-less related to a species' shade tolerance. The species that regenerated by both seeds and sprouts are, for the most, shade-tolerant or partially shade-tolerant (Pinard *et al.* 1999).

Table 4-8. Summary of treatment and regeneration mode effects on densities, heights, and RGRs of 7 commercial tree species and one non-commercial tree species (*Acosmium cardenasii*). Species are grouped into 3 classes: 1) species that regenerated from seeds; 2) species that regenerated from both seeds and sprouts; and, 3) one species that regenerated from root sprouts. Significant differences among treatments or modes of regeneration are noted as "NS." Non-significant differences are noted as "NS." Where results are significant, the treatment or mode of regeneration with the highest values (i.e., most abundant, tallest, or highest RGR) are noted. Treatments codes are: 1=high intensity burn; 2=low intensity burn; 3=plant removal; 4=gap control; and, 5=forest understory. Regeneration modes are symbolized by seedlings (sd), sprouts (sp), and root sprouts (rs). Results of statistical tests summarized in this table are displayed in Tables 4-3, 4-4, and 4-5, or in the text.

Species and regeneration groups	Treatment effects						Mode of regeneration					
	Density[a]		Height[b]		RGR		Density abundant		Height tallest		RGR highest	
	sig. (trt. with most)		sig. (trt. with tallest)		sig. (trt. with highest)		sig. (abundant mode)		sig. (tallest mode)		sig. (highest mode)	
	sig.	trt. with most	sig.	trt. with tallest	sig.	trt. with highest	sig.	mode	sig.	mode	sig.	mode
1) Seedlings only												
Anadenanthera colubrina	S	5, 3[c]	S	1	S	1	N/A	sd			NS	
Astronium urundueva	S	1	NS		NS		N/A	sd				
2) Both seedlings and sprouts												
Caesalpinia pluviosa 1st cohort												
seedlings	S	3	NS[d]		NS		NS		S	sp	NS	
sprouts	NS											
Caesalpinia pluviosa 2nd cohort												
seedlings	NS		NS		NS		N/A					
sprouts	NS		NS		NS		S	sd	S	sp	NS	
Copaifera chodatiana												
seedlings	S	3, 4, 5	NS		NS		S	sd	S	sp	NS	
sprouts	NS											
Aspidosperma rigidum												
seedlings	S	5	NS		NS		S	sp	S	sp	NS	
sprouts	S	2										

Table 4-8. (cont.)

Species and regeneration groups	Treatment effects						Seedlings vs. resprouts					
	Density		Height		RGR		Density		Height		RGR	
	sig.	trt. with most	sig.	trt. with tallest	sig.	trt. with highest	sig.	abundant mode	sig.	tallest mode	sig.	highest mode
Acosmium cardenasii												
seedlings	S	5, 4	S	4	S	1, 2	NS		NS		NS	
sprouts	S	3, 2										
3) Root sprouts												
Centrolobium microchaete												
seedlings (sown)	S	1	NS		NS		S	rs	S	rs	S	rs
root sprouts	S	2, 3										

a = Kruskall-Wallis tests were used to compare densities of all species except *Anadenanthera* and *Acosmium*.

b = ANOVA models with treatment and mode of regeneration as factors were used to test heights and RGR's. If the treatment*mode of regeneration interaction was not significant, seedlings and saplings were not analyzed separately.

c = most abundant in the forest after 3 months, most abundant in plant removal treatment after 18 months.

"N/A" Statistics not performed, all seedlings

Characteristic of shade-tolerant species, they had seedling banks in forest understories before treatments (Table 4-2), and therefore a pool of individuals from which to sprout. *Anadenanthera* and *Astronium* show shade-intolerant characteristics and their pre-gap seedling densities were low (Table 4-2), offering no structures from which to sprout. These species also had abundant seed fall in 1997, and moderate to high germination rates, creating a large seedling cohort the first year of this study.

Centrolobium, which regenerated primarily as root suckers, provides an exception to these 2 groups. Sprouts of *Centrolobium* did not originate from the seedling bank (pre-gap seedling densities of *Centrolobium* were very low- none were encountered in the 1995 inventory; Killeen *et al.* 1998), but from the root systems of mature trees. Although seedlings of *Centrolobium* did establish in all treatments, apparently none of these seedlings were from naturally dispersed seeds; natural regeneration of *Centrolobium* consisted only of root suckers. Similarly, regeneration of *Platymiscium ulei* was only encountered as root suckers and may have the same regeneration strategy as *Centrolobium*.

Gap treatment effects on density and survival

Species regenerating as seedlings only. Because the conditions that favor seedling establishment may not be the same as those that favor sprouting, density of regeneration among species varied according to their predominant mode of regeneration. The species that regenerated as seedlings, *Anadenanthera* and *Astronium,* were most abundant in treatments that favored their seedling establishment and survival, although initially the optimal treatment differed among these two species.

Astronium seedlings were most abundant after high-intensity burns and absent from forest and gap control plots, a pattern that suggests *Astronium* seedlings are unable to establish or survive under shade or need exposed soils to germinate and establish. Although canopy cover > 2 m tall in gap control plots was similar to the other gap treatments (Chapter 2), colonizing plant

cover < 2 m tall was almost 100% within less than 6 months following burns (Chapter 5). Cover by low vegetation potentially has a more negative impact on newly emerging seedlings than cover higher in the canopy (Marquis *et al.* 1986). Similarly, Kennedy and Swaine (1992) showed that experimental removal of advance regeneration resulted in increased survival of seedlings that colonize gaps from seed in lowland dipterocarp forests. Initial plant cover was zero in treatment plots with *Astronium* recruitment (plant removal and burn treatments). In high-intensity burn treatments, where *Astronium* recruitment was greatest, total plant cover remained low (< 25%) throughout the first year (Chapter 5).

In contrast, *Anadenanthera* seedlings were initially most abundant in forest plots. This density pattern is likely a combination of higher seed fall into forests than gaps (Chapter 5) and, unlike *Astronium*, the ability of *Anadenanthera* seedlings to persist in shade. However, due to high mortality of *Anadenanthera* seedlings in forest understories, patterns of seedling distribution among treatments may resemble those of *Astronium* after several years. During the first year of this study, forest seedling densities declined to levels similar to gap treatments. Also, although a density of 0.05 seedlings/m^2 was found in 1995 in this same forest (Killeen *et al.* 1998), I did not encounter any seedlings older than the 1997 cohort in forest plots, supporting the idea that seedlings of *Anadenanthera* are short-lived in the shade. Seedling survival in the second year of the study was highest in high-intensity burn treatments, possibly due to the larger size of these seedlings (Lieberman 1996). Therefore, seedling density after several years may be highest in this treatment.

Enhanced seedling establishment or survival of *Astronium* and *Anadenanthera* in the burned and plant removal treatments can be attributed to a variety of factors, including reduced competition, removal of slash and litter, and/or soil disturbance. In other neotropical forests, the abundance of species colonizing from seed have been shown to increase in canopy gaps that have been further disturbed by either logging or fire. In dry forests of Mexico for example, Dickinson

(1998) found that colonizing seedling density in logging gaps traversed by skidders was more than double that in logging gaps not disturbed by skidders. Similarly, high densities of pioneer seedlings were reported to establish in canopy opening after fire in Amazonian Brazil (Holdsworth and Uhl 1997). However, in these studies, the effects of soil disturbance and litter removal by fire or logging were not independent of reduced competition due to removal of established vegetation (Dickinson 1998). Removal of advanced regeneration from gaps in my study (plant removal treatment) resulted in higher seedling densities of *Anadenanthera* than burned treatments, but lower densities of *Astronium*. Therefore, the effects of microsite on seedling establishment vary even among species with similar regeneration strategies.

Although early seedling density is a function of seed germination and establishment, long-term seedling density is more affected by survival. As previously discussed, greater survival of *Anadenanthera* seedlings after high-intensity burns will likely result in higher seedling densities in this treatment. Hence, microsite conditions that favor germination and establishment do not necessarily benefit subsequent growth and survival. Similar conclusions were reached by Stanley (1999) who found that although seed germination of *Swietenia macrophylla* was lower in burned than unburned gaps, subsequent seedling growth rates were higher.

Species regenerating as root sprouts. Natural regeneration of *Centrolobium* was most abundant in the plant removal and burn treatments, suggesting these treatments favor root sprouting. Similarly, root sprouts of *Platymiscium uleii* were found only in the plant removal and burn treatments. Root sprouting in *Fagus grandifolia* (American beech) developed after roots were injured or exposed to air or elevated temperatures (Jones and Raynal 1988), conditions likely to occur in the plant removal and burn treatments. Similarly, Dickinson (1998) found that traversal by skidders during logging operations promoted subsequent root sprouting by several dry forest tree species in Mexico. Root damage can lead to the formation of callus, tissue from which adventitious buds and sprouts arise (Jones and Raynal 1988). Root-sprouting may also be

promoted by the loss of apical dominance (e.g., for *Populus tremuloides*; Schier 1975). This mechanism would account for high densities of root sprouts in gap control plots where stumps of harvested *Centrolobium* were located. Loss of apical dominance would also explain intermediate frequencies of root sprouts in logging gaps that were not traversed by skidders in Dickinson's study (1998).

Species regenerating as both seedlings and sprouts. Density patterns of species regenerating as both seedlings and sprouts (*Acosmium, Copaifera, Caesalpinia, Aspidosperma*) differed according the regeneration mode. Of this group, *Acosmium* revealed the most distinct response, made more clear perhaps by its high abundance. *Acosmium* had the highest pre-treatment density (0.7 seedlings/m^2 in forest plots in a 1995 inventory; Killeen *et al.* 1998). The density of seedlings and sprouts in my study largely reflect what happened to this seedling bank during treatments. Seedlings were mostly undamaged in forest understorys and gap controls, therefore the highest seedling densities were found in these areas. All seedlings were damaged in the low-intensity burn and plant removal treatment, rendering sprouts more common in these treatments. Seeds and stems were likely killed in the high-intensity burn treatment, resulting in the lowest densities for both seedlings and sprouts in this treatment. Seedling densities of *Copaifera, Aspidosperma,* and *Caesalpinia* were also highest in the less disturbed treatments.

Patterns of regeneration among these species stresses the important role advance regeneration plays in determining the success of shade-tolerant species following disturbances. Where advance regeneration is abundant, less intense disturbances such as canopy gap formation will favor these species. However, more intense disturbances, such as severe fire, may kill advance regeneration thus favoring species that colonize from seed. Dickinson (1998) reported similar results in his study in Mexico. Shade-tolerant species were most abundant in forest understories and natural canopy gaps, but in logging gaps, skidder damage reduced the abundance of these species.

Interestingly, sprout density of *Aspidosperma* was highest in the burned treatments. This pattern may be due to its ability to survive fire. Based on its bark thermal properties and thickness, *Aspidosperma* was classified as the most fire resistant among the species focused on in my study (Pinard and Huffman 1997). Survival by sprouting among the other shade-tolerant species in high-intensity burn plots was comparatively low, again possibly due to their bark characteristics. *Acosmium, Copaifera,* and *Caesalpinia* were classified among the least fire-resistant among canopy trees in Lomerio (Pinard and Huffman 1997).

Gap treatment effects on heights and RGRs

Treatment effects on the height and RGR of individuals of a particular species also are more clearly interpreted in terms of the species' regeneration strategy by seeds, sprouts, or a combination of both. In general, species that regenerated primarily by seed (*Anadenanthera, Astronium*) revealed patterns of treatment effects on height, while species that regenerated by sprouting (*Centrolobium*) or a combination (*Caesalpinia, Copaifera, Aspidosperma*) did not show significant treatment effects (Table 4-8).

Species regenerating as seedlings only. Seedlings of both *Anadenanthera* and *Astronium* were tallest in high-intensity burn plots and average height decreased with decreasing treatment intensity. Similarly, Stanley (1999) found that relative height growth of *Swietenia* seedlings was greater in burned than unburned gaps in Guatemala. High growth rates of seedlings establishing after high-intensity burns is not unexpected, because this treatment had the slowest recovery of vegetation among all gap treatments (Chapter 5) and therefore less above- and below-ground competition. In addition to less below-ground competition, soil sampled from the high-intensity burn treatment had higher availability of ammonium, nitrate, and phosphorous, as well as higher cation concentrations (Ca, Mg, and K; Chapter 3).

It is not clear from this study which factor had more of an effect on seedling growth, increased light availability or increased soil nutrients. Seedlings of *Anadenanthera* were taller in

gap centers than gap edges, which suggests that even slight increases in light availability can enhance seedling growth. On the other hand, by comparing *Anadenanthera* seedling height in the low-intensity burn and plant removal treatments, an argument can also be made for a positive effect of increased soil nutrients on seedling height. Recovery of vegetation after low-intensity burn and plant removal treatments was not significantly different (Chapter 5), but soils sampled after low-intensity burns had significantly higher concentrations of soil nutrients (Chapter 3). The greater height of *Anadenanthera* seedlings in low-intensity burn treatments suggests that below-ground effects may also significantly increase seedling growth.

Many studies have addressed the importance of above- vs. below-ground effects on seedling growth. In greenhouse studies, Kitajima (1992) showed that light availability was the primary factor limiting seedling growth in a cross-factorial experiment controlling nutrient or water supply with light availability. Conclusions drawn from field studies reveal that the relative importance of below-ground effects vary according to the site and species in question. In dry forests, reduced below-ground competition appears to benefit seedling growth. For example, in a study conducted in a dry forest in Costa Rica, Gerhardt (1995, 1996) reported that root trenching increased seedling growth of 4 tree species during the rainy season and increased their survival during the dry season. In a similar study conducted in a dry forest in Mexico, Dickinson (1998) found that seedling height of *Swietenia macrophylla* increased in response to reduced root competition. Studies conducted in infertile sites also conclude that below-ground competition may limit seedling growth (e.g., Putz and Canham 1992, Coomes and Grubb 1998).

In contrast to the results from dry or infertile forest sites, studies conducted in La Selva, a wet forest with high soil fertility, report that soil resources do not significantly limit seedling growth (Ostertag 1998, Denslow *et al.* 1990). Correspondingly, Pooter (1998), working in a moist Amazonian forest in Bolivia, found that watering tree seedlings during the dry season did not enhance growth.

Species regenerating as both seedlings and sprouts. Among most of the species regenerating as both seedlings and sprouts, there was no effect of treatments on height or RGR (Table 4-8). This pattern may be because any possible treatment effects were obscured by the tremendous height differences between seedlings and sprouts. Sprouts were taller than conspecific seedlings therefore the height of an individual was more dependent on if it was a seedling or sprout rather than the treatment where it was located. This lack of significance may also have reflected a real lack of difference in seedling or sprout growth among treatments. Growth of sprouts may have been less influenced by treatments because they depend on stored carbohydrate reserves in roots and therefore are less affected by above- and below-ground competition during early developmental stages.

Seedling growth of these particular species may have been less affected by treatments than seedlings of *Anadenanthera* and *Astronium* because they are more shade-tolerant. Shade-tolerant species, which have slower acclimation rates than shade-intolerant species (Kitajima 1996), grow more slowly even in high light (e.g., Denslow 1987, Denslow *et al.* 1990). Perhaps due to their slower growth, treatment effects on seedling height and RGR were not apparent after 18 months for these shade-tolerant species. Also, differences in below-ground effects among treatments may have been less important for shade-tolerant species due to their slower growth rates. The relative importance of below-ground effects differs among shade-tolerant and intolerant species. In Dickinson's study (1998), reduced root competition did not increase seedling height of a shade-tolerant species, as it did for *Swietenia*. Also, Denslow *et al.* (1998) reported that whereas light-demanding species responded better to increased soil nutrients in high light, shade-tolerant species showed no response.

Species regenerating as root sprouts. There were a greater differences in height and RGR between seedlings and root sprouts of *Centrolobium* than observed in the other species that regenerated from both seeds and sprouts. *Centrolobium* root sprouts were more than 7 times taller

than conspecific seedlings. *Centrolobium* sprouts also were taller than sprouts of other commercial species and there were more *Centrolobium* sprouts > 2.5 m tall in the treatment plots than of any other tree species, commercial or non-commercial (Chapter 5). *Centrolobium* sprouts may grow more rapidly than sprouts of other species because they sprout from the root systems of mature trees and therefore have larger carbohydrate reserves to utilize than sprouts of other species, which mostly originated from juveniles.

Advantages of early colonization for seedling growth and survival

Seedling density, height, and RGR of the '98 cohort of *Caesalpinia* did not differ among treatments, possibly reflecting that after 1 year, colonizing vegetation had obscured treatment effects. Within 18 months, plant cover < 2 m was greater than 60% in all gap treatments (Chapter 5). A rapid regrowth of vegetation is often observed after canopy gap formation or other disturbances in many tropical forests. For example, Thompson *et al.* (1998) reported that gap area (as defined by vegetation > 2 m tall) was reduced by 85% within only 4 years after gap formation in an Amazonian forest. Due to this rapidly colonizing vegetation, light, temperature, and relative humidity often to return to pre-gap levels within the first or second year after gap formation (e.g., Denslow *et al.* 1987).

Where areas opened by disturbance are quickly recolonized, early establishment is vital to the success of regenerating individuals. Individuals establishing early often enjoy greater resource availability than those establishing later (Canham and Marks 1985), and as a result, growth and survival rates are reported to be higher for plants establishing soon after canopy gap formation in the tropics. For example, in treefall gaps in Panama, early recruits of both pioneers and primary forest species grew faster than later recruits (Brokaw 1985a).

Often, it is the individuals that were present before disturbance (i.e., advance regeneration) that are the most successful. For example, Uhl *et al.* (1988b) found that advance regeneration accounted for 97% of all trees > 1 m tall in single treefall gaps and 83% in multiple treefall gaps 4

years after gap formation in Amazonia. Similarly, Brown and Whitmore (1992) reported that the most important determinant of seedling survival and growth in treefall gaps in Borneo was seedling size at the time of gap creation, regardless of species. The patterns of seedling and sprout density among the shade-tolerant species in this study suggest that these species rely mostly on advance regeneration following disturbances of low to medium intensity.

The general success of early recruits has important implications for studies, such as this one, that examine regeneration only for short time periods. Early survivorship has been shown to be a good indicator of subsequent survivorship for periods up to 6 years of age (Li *et al.* 1996). To the extent that individuals or species that are successful during the first year or two will continue to dominate over later recruits, the future success of species in this study can be predicted based on their survival rates and height 18 months following gap treatments. For example, seedlings of *Anadenanthera* and *Astronium* will likely be most successful in the high-intensity burn treatment. Root sprouts of *Centrolobium* will likely dominate individuals of other commercial tree species, particularly in gaps formed by a harvested mature *Centrolobium*. Shade-tolerant species (*Acosmium, Caesalpinia, Aspidosperma*, and *Copaifera*) will be most successful in gap controls, and sprouts of these species will likely be more dominant (i.e., larger) than conspecific seedlings.

Implications for management

Variation among species' responses to gap treatments in this study reinforces the conclusion of Pinard *et al.* (1999) that one management system cannot be applied to enhance the regeneration of all timber species within this forest site. They suggested a mixed management scheme is most appropriate with this mixture of species, proposing an even-aged management system for the shade-intolerant species (*Anadenanthera, Astronium, Centrolobium*, and *Schinopsis)*, involving the creation of large multiple-treefall gaps, and an uneven-aged management system for the shade-tolerant species (*Caesalpinia, Aspidosperma*, and *Copaifera)*, involving the creation of smaller single-treefall gaps.

However, the results of this study suggest that even large, multiple-treefall gaps may not provide suitable habitat for shade-intolerant species. Poor recruitment of *Anadenathera* and *Astronium* seedlings in gap control plots suggest that advance regeneration, logging debris, and deep litter in treefall gaps limit suitable sites for establishment and survival of these species. Therefore, selective logging without additional silvicultural treatments, such as slash removal or prescribed burning, may not be sufficient to improve regeneration of these shade-intolerant species.

Growth and survival of *Anadenathera* and *Astronium* improved with increasing treatment intensity. However, high-intensity burns may not be the most appropriate silvicultural treatment for regenerating these species. High-intensity burns will negatively affect species that depend on seedling banks for regeneration. Growth and survival of shade-intolerant species after low-intensity burns, while lower than after high-intensity burns, may be sufficient for management purposes. If burns are prescribed, they must be timed before peak seedfall, as burns of high and low-intensity decrease seed viability of seeds in the seed bank.

This study also supports conclusions drawn by other researchers that advanced regeneration is the important source of post-disturbance regeneration among shade-tolerant species. In this study, most advance regeneration was killed by high-intensity burns. The importance of advance regeneration creates a conflict between promoting regeneration of shade-intolerant species with intense silvicultural treatments while trying to maintain regeneration of shade-tolerant species. If advanced regeneration of shade-tolerant species is abundant within a particular area, then intensive silvicultural treatments such as prescribed burns would not be appropriate. Other less intense treatments that would release seedlings/saplings of competition, such as weeding and/or thinning, would be more suitable.

CHAPTER 5
EFFECTS OF CANOPY GAP FORMATION, PLANT REMOVAL, AND
CONTROLLED BURNS OF HIGH AND LOW INTENSITIES ON
A DRY FOREST PLANT COMMUNITY

Introduction

Patterns of forest regeneration following natural or anthropogenic disturbances are determined by interactions between the disturbance regime (i.e., intensity, frequency, scale) and the biologies of species (i.e., life history, physiology, behavior; Pickett and White 1985). Disturbances that differ from the historic disturbance regime either in type, frequency, intensity, or scale may not only decrease species diversity but may also shift the community to one dominated by a few tolerant species or life forms (e.g., Connell 1978, Denslow 1995, Roberts and Gilliam 1995). For example, vines often dominate tropical forests after uncontrolled logging (Dawkins 1961) and grasses may dominate for decades after pasture abandonment (Uhl *et al.* 1988a).

Shifts in species composition following disturbances arise, in part, from differences in species-specific modes of persistence through these disturbances. Modes of regeneration, i.e., from sprouts, seedling banks, seed banks, or dispersed seeds, may influence the success or dominance of a species in successional communities. Although regeneration from seed has received more attention from researchers, in tropical forests, sprouting is also a common means of persistence through disturbance (Stocker 1981, Uhl and Jordan 1984, Putz and Brokaw 1989, Kaufmann and Uhl 1990, Kaufmann 1991). In tropical dry forests, frequencies of sprouting are thought to be even higher than in wet tropical forests (Ewel 1980, Sampiao *et al.* 1993, Murphy and Lugo 1986, Hardesty 1988, Miller and Kaufmann 1998a,b).

The importance of sprouting as a means of survival varies within a site as well among forest types, depending on the intensity of disturbance. Several studies show that frequency of sprouting declines with increasing severity of disturbance. For example, in both wet and dry tropical forests, sprouts were less common after slash burning than after less intense disturbances (Sampiao *et al.* 1993 Miller and Kaufmann 1998a, b, Kaufmann 1991, Uhl *et al.* 1981, Uhl and Jordan 1984). Regeneration from seed may also be affected by disturbance intensity. While less intense disturbances such as canopy opening may stimulate many seeds to germinate (e.g., Vazquez-Yanes and Orozco-Segovia 1993), more severe disturbances, such as intense fires, kill seeds buried in surface soils (Brinkmann and Vieira 1971, Uhl *et al.* 1981). Therefore, it is often colonizing species that regenerate via widely dispersed seeds that dominate following disturbances of high intensity (Uhl *et al.* 1981, Schimmel and Granstrom 1996).

Modes of regeneration not only determine survival through a disturbance, but also influence growth and survival following disturbance. Due to their larger carbohydrate reserves, sprouts may form larger, taller crowns more rapidly than seedlings (Miller and Kauffman 1998b). And, although few studies have directly compared survival of seedlings and sprouts, their survival rates are also likely to differ. While mortality of both seedlings and sprouts may be affected by herbivores (Moreno and Oechel 1994) or fungal pathogens (Wenger 1951, Augsperger 1983), mortality of seedlings is more dependent on external factors such as light availability (Veenendall *et al.* 1995, Thompson et al. 1998, Kitajima 1994) and soil moisture (Gerhardt 1996). Sprout mortality, at least initially, is correlated with internal factors such as the size or age of the original stem, height and extent of stem damage, and number of sprouts sharing the same root system (Wenger 1951, Blake 1983).

In this chapter, I characterize early successional patterns following canopy opening, plant removal, and controlled burns of high and low intensity. I focus on the dominance of species, life forms, and alternate regeneration modes (i.e., from seed or by sprouting). In these studies, I define

dominance by various measures of size (stem height and diameter) or cover (percent cover and crown area). Specifically, my objectives are: 1) to examine the effects of gap formation, above-ground plant removal, and high and low-intensity burns on soil seed banks and to quantify new seed fall into gaps following these treatments; 2) to compare the effects of these treatments on the relative cover of different life forms; 3) to document the species, lifeform, and mode of regeneration of dominant individuals in these treatments; 4) to compare the relative dominance of seedlings and sprouts among these treatments; and, 5) to compare species richness among the treatments.

Methods

The studies described in this chapter were carried out in the high-intensity burn, low-intensity burn, plant removal, gap control, and forest plots described in Chapter 2.

Seed bank and seed rain studies

Effects of gap treatments on soil seed banks. To examine treatment effects on seeds stored in the soil, seed bank samples were collected from each treatment the week following controlled burns. Four subsamples (20 x 20 cm, 3 cm depth) were collected from each gap treatment plot and transported to the nearby community of San Lorenzo for germination. Soil samples were spread on 10 x 50 cm trays, watered twice daily, and examined every 7 to 10 days for germinated seeds. Trays received direct sunlight during the morning and evening hours. After 11 weeks, all seedlings were collected and pressed. Most seedlings other than commercial tree seedlings were difficult to identify and were grouped by morphospecies. The total number of germinated seeds and the number of germinated seeds of commercial tree species were compared among treatments using ANOVA with treatments as fixed effects and blocks as random effects followed by Tukey's HSD post-hoc comparisons.

   Seed rain into gap centers, gap edges, and forest understories. To compare seed rain

densities into forest understories, gap edges, and gap centers, seed traps were placed at each site in

each block and monitored for 9 weeks following burns. Gap center and gap edge traps were

located 2.5 and 7.5 m from gap centers, respectively, and forest traps were located within 2-5 m of

the forest subplots. Traps were constructed of 50 x 50 cm PVC frames with a net of woven plastic

sewn to the sides. Traps were elevated 50 cm above the soil surface. Seeds were collected every 1

to 2 weeks, counted, and identified to species or morphospecies. The total numbers of seeds,

commercial tree seeds, liana seeds, and species were compared among trap locations (gap center,

gap edge, and forest understory) using ANOVA with trap location as a fixed effect and blocks as

random effects followed by Tukey's HSD post-hoc comparisons.

Effects of gap treatments on cover of different life forms

   To compare relative cover of life forms among the four gap treatments and forest plots, I

estimated percent cover 1.5, 3, 6, 9, 12, and 18 months after burns. In each 4 m^2 subplot, total

plant cover and percent cover of bromeliads, vines, grasses, herbs, shrubs, and trees was estimated

visually. In forest plots, only cover < 2 m tall was estimated. Vine cover included both herbaceous

and woody vines (lianas). Maximum total cover was limited to 100%, but where leaf cover of

different life forms overlapped, the sum of their percent covers could total >100%. Total cover

and percent cover by life form were compared among treatments using repeated measures analyses

of variance with treatments as fixed effects and blocks as random effects followed by Tukey's

HSD post-hoc comparisons.

Regeneration mode, life form, and species of tallest individuals

   To identify which species, life forms, and regeneration modes were dominant in each gap

treatment, I selected the tallest individual in each 4 m^2 subplot at 1.5, 3, 6, 9, 12, and 18 months

following, identified it to species, determined its mode of regeneration (seedling or sprout), and

measured its height. Additionally, after 9 and 18 months, I identified all individuals within each 100 m² treatment plot > 2.5 m tall, determined their modes of regeneration (seedling or sprout), and measured their heights.

Average heights of the tallest individual per 4 m² subplot were compared among treatments using repeated measures ANOVA with treatments as fixed effects and blocks as random effects followed by Tukey's HSD post-hoc comparisons. A Kruskall-Wallis test was used to compare life form and regeneration mode of the tallest individual per 4 m² subplot among treatments. For this test, proportions were calculated for each treatment plot using the four 4 m² subplots. The total number of individuals > 2.5 m tall were compared among treatments using a Kruskall-Wallis test at 9 months and an ANOVA at 18 months. The proportions of tree seedlings, tree sprouts, liana seedlings, and liana sprouts among the total number of individuals > 2.5 m tall were compared among treatments using a Kruskall-Wallis test.

Comparison of dominant seedlings and sprouts

Seedlings were not commonly the tallest individual per 4 m² subplot and few seedlings reached heights > 2.5 m. Therefore, I conducted an additional survey 9 months following burns to compare sizes of dominant seedlings and dominant sprouts. In this survey, sampling was restricted to the two center subplots of each gap treatment (two 4 m² subplots = 8 m²). Although one plot of this pair received a seed addition treatment (Chapter 4), in this survey only size, rather than density, of seedlings and sprouts are compared and therefore the seed addition treatment has minimal effect on the results. In each 8 m² area, the 5 tallest individuals of each of the following groups were identified: tree sprouts, tree seedlings, liana sprouts, and liana seedlings. For each individual, I measured the height, basal diameter, crown length (L), crown width (W), and, for sprouting individuals, the number of stems, diameter of the largest sprout, and sprout origin (root, root collar, or stem). Crown areas were estimated as:

$$\text{Area} = (L* W * 3.1416) / 4$$

Crown widths and lengths were difficult to measure for lianas that had one-to-many long climbing or scrambling stems. For these lianas, the measurement of crown length (L) was estimated by multiplying the number of stems by the estimated average length of these stems. The average width of leaves on stems was used as crown width (W).

The sizes of seedlings and sprouts sampled in the 8 m² plots were compared using ANOVAs with treatment, regeneration mode, and life form as factors. For these tests, mean heights, crown areas, stem diameters, and numbers of stems were log transformed prior to analyses. Blocks were treated as a random effect in each model. To compare the origin of sprouting (root, root collar, stem) among treatments, frequencies of each were compared among gap treatments using Kruskal-Wallis tests.

Effects of gap treatments on plant species richness and similarity

Species richness was assessed in each gap treatment 9 months following burns (June 1998). All species within each 100 m² gap treatment plot were identified for all blocks. Unknown species were collected, pressed, and identified at the herbarium in the Museo de Historia Natural de Noel Kempff Mercado in Santa Cruz. The mean number of species and the average number of grass, shrub, herb, tree, and woody and herbaceous vine species per 100 m² plot were compared among treatments using ANOVAs with treatments as fixed effects and blocks as random effects. Sorenson's similarity index (S_c) was used to compare percent similarity of species among treatments:

$$S_c = 2c / (a + b)$$

where c is the number of species in common between 2 treatments and a and b are the total number of species found in the 2 treatments.

Results

Seed bank and seed rain studies

Effects of gap treatments on soil seed banks. Total seedling density and commercial tree seedling density were highest in seed banks sampled from gap controls and lowest in high-intensity burn plots (Figure 5-1). An average of 32 (5-164) seeds m^{-2} germinated in seed banks sampled from gap controls, including 6 seeds m^{-2} of commercial tree species. In seed banks sampled from high-intensity burn plots, only 5 germinants of an unidentified species and no commercial tree species were found in all 64 seed bank samples (representing a total area of 2.56 m^2). *Ruellia* spp. (Acanthaceae), perennial herbs, were the most common species germinating in seed banks sampled from gap control, plant removal, and low-intensity burn treatments. A total of 25 morphospecies, including four commercial tree species, germinated in seed banks sampled from all treatments.

Seed rain into gap centers, gap edges, and forest understories. An average of 94 (24-212) seeds m^{-2} were caught by forest seed traps during the 9 week collection period from September 11 to November 13, 1997. Seed rain peaked the first week of October but by the third week had fallen to 2 seeds m^{-2} week^{-1}. Seed rain into gaps was only 25% of that collected in forest traps (Figure 5-1). Roughly equal numbers of seeds fell into gap center and gap edge traps. *Anadenanthera colubrina*, a commercial species, had the most abundant seed fall. Of the total 181 *Anadenanthera* seeds collected, 77% fell into forest traps, 14% into gap edge traps, and 9% into gap center traps. Distribution of *Astronium urundueva* seed rain, also a commercial species, was more even; of the total 94 *Astronium* seeds collected, 29% fell in gap center traps, 35% into gap edge traps, and 36% into forest traps. *Thiloa paraguariensis* (Combretaceae) had the most abundant seed rain of vines; of the total 154 seeds collected, 66% fell into forest traps, 12% into gap edge traps, and 21% into gap center traps.
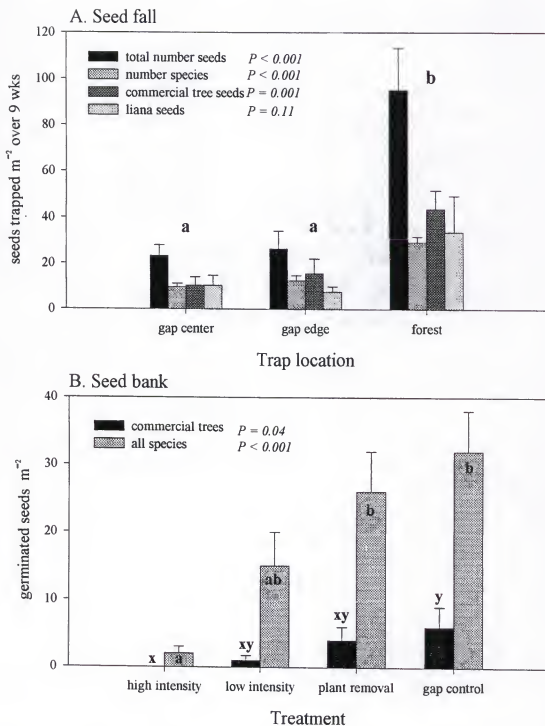
Figure 5-1. A. Numbers of seeds, species, commercial tree seeds, and liana seeds captured in 0.25 m² seed traps placed in forest, gap center, and gap edges for 9 weeks following treatments. B. Density of seeds of all species and of commercial tree species in seed banks sampled to 3 cm depth in the four gap treatments. In both graphs, different letters indicate significant differences at P < 0.05. Bars represent standard errors (n = 16).

Effects of gap treatments on cover of different life forms

Total plant cover. Total cover increased greatly in all gap treatments over the 18 month post-burn sampling period and significantly differed among treatments (Table 5-1). Total cover in the high-intensity burn treatment remained the lowest at all sampling periods, increasing from 1% at 6 weeks to 65% at 18 months (Figure 5-2). Total cover in gap controls remained the highest, increasing from 47% at 6 weeks to 100% at 18 months. Relative increases in total cover in the low-intensity burn and plant removal treatments were the greatest; they increased from 7% to 90% and 14% to 95%, respectively. Plant cover < 2 m in forest understory plots did not increase over the duration of the study but varied seasonally, ranging from 46% during the dry season to 62% during the wet season.

Percent cover of life forms. There were significant differences among treatments in percent cover of trees, herbaceous and woody vines, shrubs, herbs, and ground bromeliads (Table 5-1 and Figure 5-2). Percent cover of ground bromeliads was highest in forest and gap control plots. Also, forest plots tended to have higher shrub cover and less herb, vine, and tree cover than gap treatments. Differences in percent cover of herbs, vines, and trees among gap treatments closely reflected differences in total cover. For example, if total cover was highest in gap control plots, so was percent cover of herbs, vines, and trees. Grass cover was low in all treatments (< 5%).

Two herbaceous species showed positive responses to burning. One species, *Commelina* sp., a perennial monocot that sprouts vegetatively from subterranean bulbs, covered an average of 14% (75% of total plant cover) of low-intensity burn plots 6 months after burns, significantly more than in any other treatment (P < 0.001). Cover of this species declined in successive sampling periods. Another species, an unidentified annual herb in the Euphorbiaceae, established only on the edges of the high-intensity burn plots and in the more intensely burned patches of the low-intensity burn plots, suggesting its seeds are stimulated by

Table 5-1. Results of ANOVA and Tukey's post-hoc tests of total cover, percent cover by lifeform, and height of the tallest individual in 4 m^2 subplots at 5 measurement periods after burns. All variables showed a significant treatment*time interaction when tested with a repeated measures model, therefore each was tested separately by month. Distribution of bromeliad percent cover was not normal, therefore this variable was tested with a Kruskall Wallis test. Cover at 6 weeks was not tested due to the high number of cells containing zeros. Treatments with different letters are significantly different at $P < 0.05$.

Total cover Months	F	P	high intensity burn	low intensity burn	plant removal	gap control	forest
3	98.7	0	a	b	b	c	c
6	70.6	0	a	b	bc	c	c
9	77.4	0	a	b	c	d	b
12	58.7	0	a	b	c	d	b
18	36.7	0	a	b	c	b	a

Tree cover Months	F	P	high	low	removal	control	forest
3	3	0.025	a	ab	b	ab	ab
6	7.9	0.000	a	b	b	ab	a
9	8.4	0.000	ab	c	c	bc	a
12	5.4	0.001	ab	b	b	b	a
18	10	0.000	ab	b	b	b	a

Herbaceous and woody vine cover Months	F	P	high	low	removal	control	forest
3	16.7	0.000	a	ab	b	c	ab
6	14.6	0.000	a	b	b	b	a
9	7.5	0.000	a	b	b	b	a
12	10.5	0.000	a	b	b	b	a
18	12.4	0.000	b	c	bc	bc	a

Herb cover Months	F	P	high	low	removal	control	forest
3	5.8	0.000	a	ab	ab	c	bc
6	21.3	0.000	a	bc	cd	d	b
9	39.3	0.000	a	b	c	c	b
12	35.9	0.000	a	a	b	b	a
18	10.4	0.000	a b	bc	c	c	a

Table 5-1. continued.

Shrub cover

Months	F	P	high	low	removal	control	forest
3	31.4	0.000	a	a	a	a	b
6	26.3	0.000	a	ab	b	b	c
9	16.2	0.000	a	ab	ab	b	c
12	16.9	0.000	a	ab	b	b	c
18	15.8	0.000	a	ab	ab	b	c

Bromeliad cover

Months	X^2	P
3	56.2	0.000
6	52.9	0.000
9	56	0.000
12	55.9	0.000
18	53.2	0.000

Tallest individual per 4 m^2 subplot

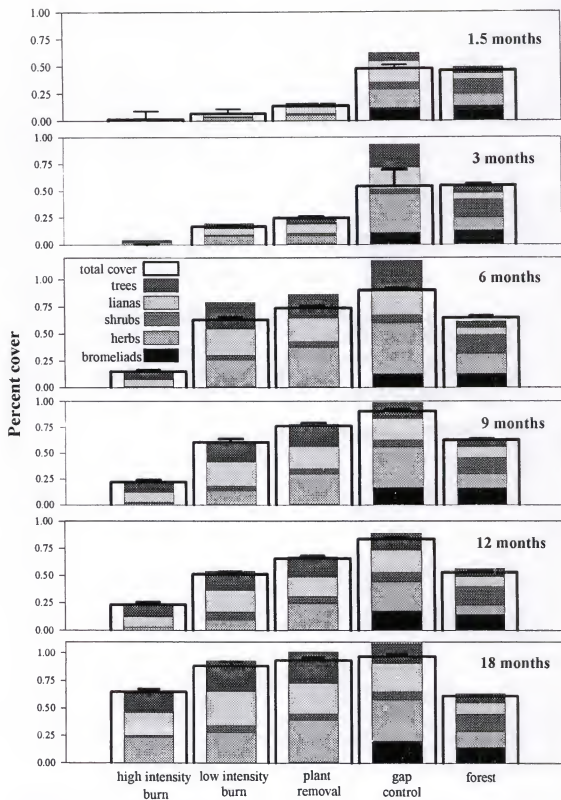| Months	F	P	high	low	plant removal	control
1.5	55.9	0.000	a	b	c	d
3	48.7	0.000	a	b	c	d
6	22.1	0.000	a	b	b	bc
9	21.7	0.000	a	b	c	bc
12	16.1	0.000	a	b	b	b
18	1.3	0.28				

Figure 5-2. Percent cover of bromeliads, herbs, shrubs, lianas, trees, and total cover (empty box) in 4 m² subplots at 1.5, 6, 9, 12, and 18 months following treatments. Bars on total cover are standard errors (n = 16). Where cover of different lifeforms overlapped, the sum their percent cover could exceed total plant cover.

fires of intermediate intensity (treatment difference: P < 0.001). Individuals of this species died after they set seed during 6-9 months following burns.

Regeneration mode, life form, and species of tallest individuals

Tallest individuals in 4 m^2 subplots. At 6 weeks, average height of the tallest individuals per 4 m^2 subplot was greatest in gap controls (Figure 5-3, Table 5-1); after 18 months, there were no differences among treatments. After 9 months, sprouts were most frequently the tallest individual per subplot in the gap control, plant removal, and low-intensity burn plots; in high-intensity burn plots, seedlings were most frequently the tallest (Figure 5-3, Table 5-2). After 6 months, commercial tree species were more frequently the tallest individuals in high-intensity burn plots than in other treatments (Figure 5-4, Table 5-2). After 9 months, non-commercial tree species were more frequently the tallest individuals in gap control, plant removal and low-intensity burn plots than in high-intensity burn plots. Sprouts of *Mimosa* sp., a scrambling shrub, were most frequently the tallest individuals in the 4 m^2 plots (Table 5-3). The second most frequent species was *Centrolobium microchaete*, a commercial tree species that suckered from roots.

Individuals > 2.5 m tall in 100 m^2 treatment plots. All of individuals > 2.5 m tall 9 months following treatments were sprouts (Figure 5-5). Of these sprouts, 90% were trees, the remaining 10% were lianas. At 9 months, the plant removal treatment had the most individuals > 2.5 m, with 3 per 100 m^2 ($X^2 = 8.8$, P = 0.03). After 18 months, the number of individuals > 2.5 m averaged 6 per 100 m^2 and did not differ among treatments (F = 0.8, P = 0.50). Seedlings comprised 40% of individuals > 2.5 m in high-intensity burn plots, a proportion slightly but not significantly higher than other treatments ($X^2 = 7.7$, P = 0.051). The most common individuals > 2.5 m tall were *Centrolobium microchaete* (Table 5-4). The second most common species > 2.5 m tall was *Mimosa* sp.. *Anadenanthera colubrina*, the third most abundant species, was found predominately as seedlings. Other common species whose

A. Average height of tallest plants in each subplot

B. Proportion of sprouts among tallest plants in each subplot
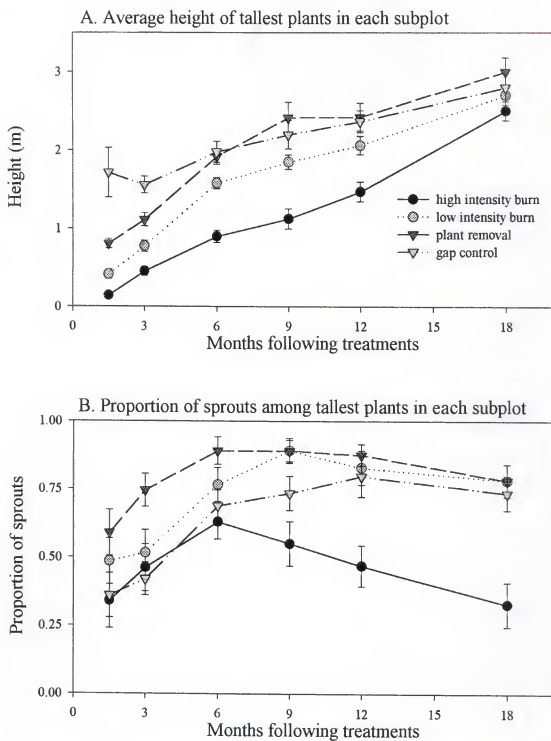
Figure 5-3. A. Average height, and (B) proportion of sprouts among tallest individuals per 4 m^2 subplot. Bars represent standard errors (n = 16).

Table 5-2. Kruskall-Wallis analyses testing whether the likelihood of a particular lifeform being the tallest individual per 4 m² subplot differs among treatments (df = 3). Sprouts similarly analyzed.

Month	commercial trees		non-comm. trees		lianas		herbs		shrubs		sprouts	
	X^2	P	X^2	P	X^2	P	X^2	P	X^2	P	X^2	P
1.5	1.4	0.69	5.6	0.13	5.4	0.14	19.6	0.0	3.7	0.30	3.7	0.29
3	5.5	0.14	4.4	0.23	1.4	0.72	9.5	0.02	8.5	0.04	12.5	0.01
6	19.6	0.000	6.1	0.11	5.1	0.16	11	0.01	8.2	0.04	7.5	0.06
9	13.9	0.003	8.3	0.04	2.8	0.42	10.4	0.02	1.5	0.69	10.5	0.02
12	10.7	0.01	9.3	0.03	1.8	0.61	3.1	0.38	3.6	0.31	17.5	0.001
18	14	0.003	15.5	0.001	2.9	0.41	7.7	0.05	6.1	0.11	18.4	0.000
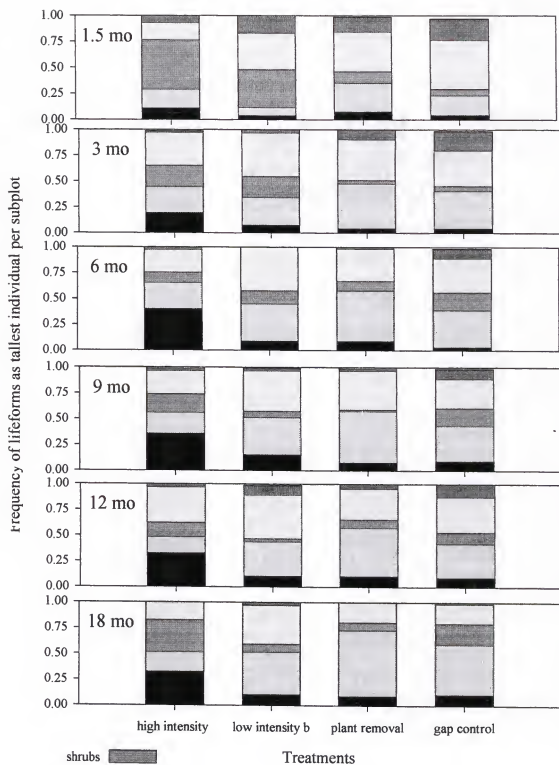
Figure 5-4. Frequency of commercial trees, non-commercial trees, herbs, lianas, and shrubs as the tallest individual per 4 m² subplot at 1.5, 6, 9, 12, and 18 months following treatments.

Table 5-3. Species recorded as the tallest individual per 4 m^2 subplot 18 months following treatments. Total number, percentage of sprouts, average height, and the frequency of each species in gap treatments are listed.

| Species	Life-form	Total #	Sprouts %	Ht. (m)	gap cont.	plant rem.	low int.	high int.
Mimosa sp.	LN	22	100	2.9	36	18	45	0
Centrolobium microchaete	CT	17	100	4.1	6	38	31	25
unknown herbs	HB	16	0	1.8	6	6	31	56
Ruellia sp.	HB	16	0	1.5	54	23	0	23
Acosmium cardenasii	TR	15	100	3.5	47	47	0	7
Acacia lorentensis	TR	12	100	5.4	17	42	25	17
Thiloa paraquariensis	LN	12	8	2.0	0	8	17	75
Anadenanthera colubrina	CT	10	20	2.2	0	0	20	80
Casearia arborea	TR	9	100	2.8	11	44	33	11
Mendoncia sp.	LN	8	63	1.9	25	38	38	0
Casearia gossyiosperma	TR	8	100	2.4	29	43	29	0
Neea hermaphrodita	TR	8	88	2.0	63	25	13	0
Spondias mombin	TR	6	100	3.0	33	0	50	17
Pogonopus tubulosus	SH	6	100	3.8	17	17	50	17
unknown lianas	LN	6	67	1.7	17	0	67	17
Caesalpinnia pluviosa	CT	6	83	2.5	50	0	33	17
Urera baccifera	TR	6	100	2.2	17	50	17	17
Trema micrantha	TR	6	0	2.8	0	67	17	17
Luehea paniculata	TR	5	100	3.2	0	40	40	20
unknown pioneer tree	TR	5	0	2.9	0	40	20	40
Bignoniaceae sp.	LN	4	50	1.7	50	25	0	25
Astronium urundueva	CT	4	0	35.1	0	0	0	100
Bauhinia sp.	SH	3	100	4.3	0	67	0	33
Manihot sp.	SH	3	100	3.0	100	0	0	0
Cordia alliodora	CT	3	100	2.0	0	0	0	100
Casearia aculata	TR	3	100	3.2	0	0	100	0
unknown vines	VN	3	100	2.0	0	0	100	0
Galipea sp.	TR	2	100	2.3	0	100	0	0
Prokia crucis	SH	2	100	2.3	0	0	100	0
Arrabidaea fagoides	LN	2	50	1.5	50	50	0	0
Zanthoxylum hasslerianum	TR	2	100	2.5	50	50	0	0
Combretum leprosum	TR	1	100	4.0	100	0	0	0
Celtis pubescens	TR	1	100	4.0	100	0	0	0
Pseudananas sagenarius	BR	1	0	1.0	100	0	0	0
Serjania marginata	LN	1	0	2.0	100	0	0	0
Aspidosperma rosado	CT	1	100	3.0	0	0	0	100
Platypodium elegans	TR	1	100	7.0	100	0	0	0
Passiflora sp.	VN	1	0	1.5	0	0	100	0
Allophyllus edulis	TR	1	100	2.0	100	0	0	0
Copaifera chodatiana	CT	1	100	1.8	0	0	100	0
Platymiscium ulei	TR	1	100	1.4	0	0	100	0
Chorisia speciosa	TR	1	100	2.5	100	0	0	0
Trigonia boliviana	LN	1	100	1.5	0	100	0	0
unknown		14						

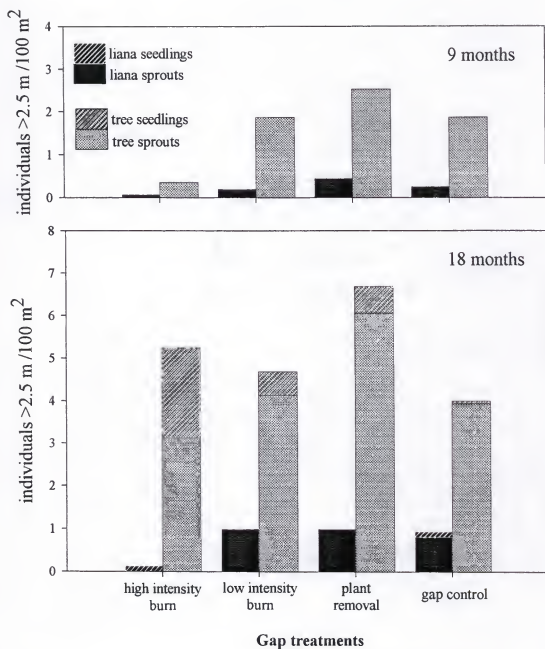CT = commercial tree, HB = herb, LN = liana, SH = shrub, TR = non-commercial tree

Figure 5-5. Number of individuals > 2.5 m tall in each 100 m² gap treatment plot after 9 and 18 months. Individuals are divided into classes based on regeneration mode (seedling or sprout) and life form (tree or liana).

Table 5-4. Species recorded > 2.5 tall in 100 m^2 treatment plots 18 months after burns. Total number, percentage of sprouts, average height, and frequency in gap treatments are listed for each species. An additional 13 species had 1 individual > 2.5 m but are not listed.

Species	Life-form	Total #	Sprout %	Ht. (m)	Frequency (%) gap cont.	plant rem.	low int.	high int.
Centrolobium microchaete	CT	67	100	4.2	18	24	15	42
Mimosa sp.	LN	35	100	3.3	29	37	34	0
Anadenanthera colubrina	CT	31	16	3.5	6	3	16	74
Acosmium cardenasii	TR	26	100	4.1	38	46	8	8
Casearia gossypiosperma	TR	26	96	3.2	32	36	0	36
Acacia loretensis	TR	25	100	5.5	16	40	40	4
Casaeria arborea	TR	14	100	3.1	14	43	36	7
Spondias mombin	TR	9	100	3.0	11	0	56	33
Zanthoxylum hasslerianum	TR	9	100	3.3	33	67	0	0
Neea hermaphrodita	TR	15	100	3.1	26	40	33	0
Trema micrantha	TR	8	0	4.8	0	50	25	25
Pogonopus tubulosus	TR	8	100	3.8	0	40	40	20
Caesalpinnia pluviosa	CT	7	100	3.0	71	0	0	29
Platymiscium ulei	CT	7	100	3.0	0	43	57	0
Urera baccifera	TR	7	71	3.3	43	43	14	0
Heliocarpus sp.	TR	7	0	4.0	0	29	29	43
Mendoncia sp.	LN	4	100	2.5	25	25	50	0
Gallesia integrefolia	TR	4	100	3.9	25	50	0	25
Cordia alliodora	CT	4	100	3.4	50	0	25	25
Bauhinia rufa	TR	4	50	4.9	0	25	0	75
Astronium urundueva	CT	4	0	3.3	0	0	0	100
Bignoniaceae sp.	LN	3	100	3.4	67	0	33	0
Galipea trifoliata	TR	3	100	3.2	67	33	0	0
Luehea paniculata	TR	3	100	4.7	0	33	33	33
Coursetia hassleri	TR	3	100	3.4	0	33	33	33
Platypodium elegans	TR	3	100	2.8	0	66	33	0
Prokia crucis	SH	3	100	2.6	0	33	67	0
Allophyllus edulis	TR	3	100	2.5	0	100	0	0
Capparis prisca	TR	2	100	3.0	0	50	50	0
Manihot sp.	TR	2	100	4.0	50	50	0	0
Combretum leprosum	TR	2	100	8.0	0	0	0	100
Bougainvillea modesta	SH	2	100	4.0	33	33	33	0
Casearia arborea	TR	2	100	3.3	0	50	50	0
Tabebuia impetiginosa	CT	2	100	2.8	50	0	50	0
Chorisia speciosa	TR	2	100	3.3	100	0	0	0
Trigonia boliviana	LN	2	100	2.8	50	0	50	0
Celtis pubescens	TR	2	50	3.0	50	0	50	0
Thiloa paraguariensis	LN	2	0	2.5	33	0	0	67

CT = commercial tree, HB = herb, LN = liana, SH = shrub, TR = non-commercial tree

seedlings reached heights > 2.5 m tall were: the trees *Trema micrantha, Heliocarpus* sp., and *Astronium urundueva*, and the vine *Thiloa paraguariensis*.

Comparison of dominant seedlings and sprouts

Tree and liana sprouts were taller (F = 8.9, P = 0.003), had more stems per individual (F = 32.1, P < 0.001), larger crown areas (F = 42.8, P < 0.001), and larger basal diameters (F = 13.4, P < 0.001; Figure 5-6) than tree and liana seedlings. Among sprouts, the origin of sprouting differed among treatments (Figure 5-7). Sprouting from roots was more common in burned plots (P < 0.001, X^2 = 25.2), sprouting from the root collar was more common in the low-intensity burn and plant removal treatments (P < 0.001, X^2 = 23.8), and sprouting from stems was the more common in the plant removal and gap control plots (P < 0.001, X^2 = 23.8).

Effects of gap treatments on plant species richness and similarity

Two-hundred and sixty-nine species and morphospecies were collected from all treatments, including: 100 vines, 64 trees, 61 herbs, 25 shrubs, 8 grasses, 2 palms, 3 cacti, 1 fern, and 1 bromeliad. Total species richness was lowest in gap controls (161 species, Figure 5-8). However, per 100 m^2 plot, fewer species were collected in high-intensity burn treatments than other treatments (F = 16.2; P < 0.001; Figure 5-9). Low-intensity burn and plant removal treatments had the highest species richness (192 and 191 species, respectively). Sorenson's similarity index revealed that the plant removal and low-intensity burn treatments shared the most species in common (161 species) while species in gap control and high-intensity burn plots were the least similar (124 species shared; Table 5-5). Frequencies of each species by gap treatment are provided in the Appendix.

Discussion

Seed bank density and seed rain following treatments

High soil temperatures created by high-intensity burns reduced densities of viable seed by an average of 94%. Average temperatures during high-intensity burns at the soil surface
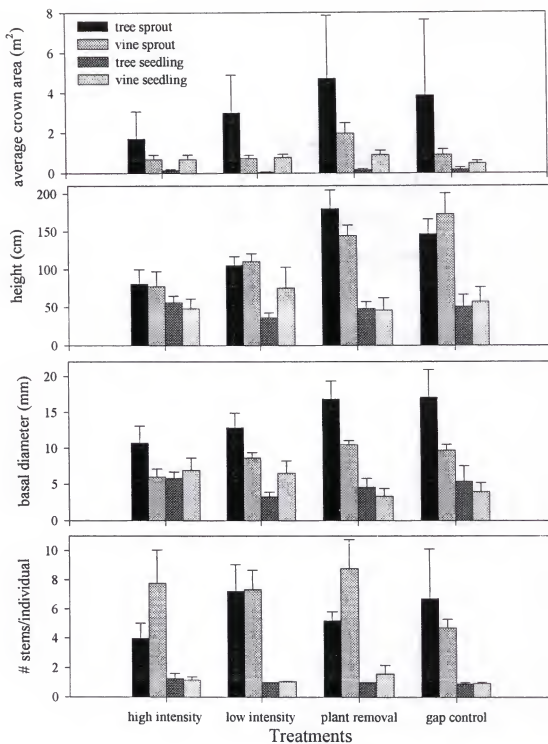
Figure 5-6. Average crown areas, heights, basal diameters of the largest new stem, and number of stems per individual of tree and vine sprouts or seedlings in each of the 4 gap treatments. Variables were measured on the 5 most dominant individuals of each group in the paired 4 m^2 center plots in each treatment of 11 blocks 9 months following burns.
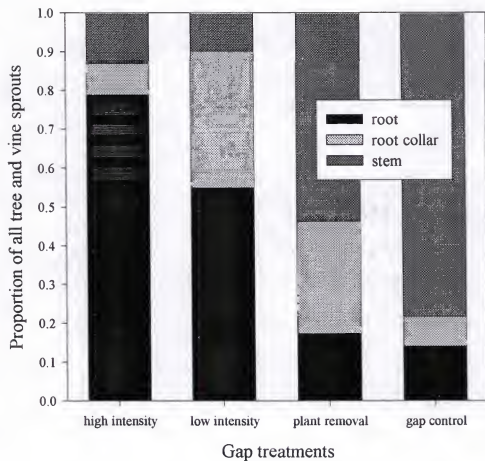
Figure 5-7. Frequency of sprouting from roots, root collars, or stems in the 4 gap treatments. Proportion of each sprout origin was taken from the entire sample of tree and vine sprouts measured in the paired 4 m^2 center plots of 11 blocks 9 months following burns.
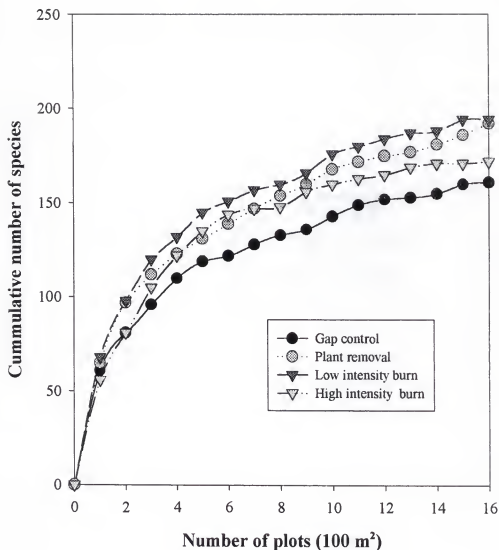
Figure 5-8. Species-area curves for each gap treatment. Each curve represents the cummulative number of species with each additional 100 m^2 plot. Plots were added in the sequence that maximized decreasing order of new species.
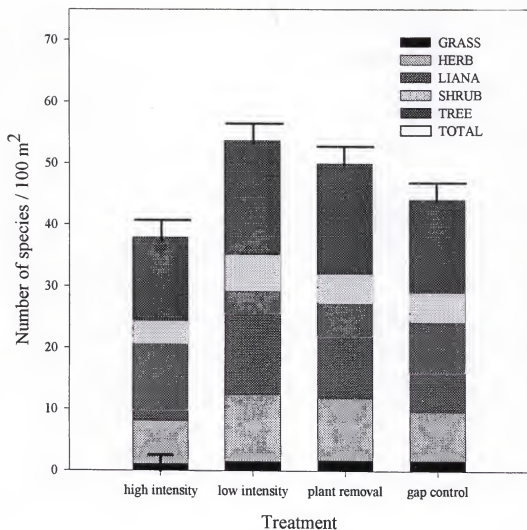
Figure 5-9. Average species richness (number of species) for grasses, herbs, lianas, shrubs, and trees in each gap treatment 9 months following burns (n = 16). Error bars represent the standard error of total species richness per plot.

Table 5-5. Similarity of species recorded in the four gap treatments. The first matrix is the tot. number of species in common between two treatments. The second matrix is Sorenson's similarity index (Sc) or percent similarity between two treatments. Sc = 2c / (a + b), where c is the number of species in common between two treatments, and a and b are the total number of species found in each of the two treatments.

	Gap control	Plant removal	Low intensity burn	High intensity burn
Gap control		138	137	124
Plant removal			161	137
Low itensity				145
High intensity				

	Gap control	Plant removal	Low intensity burn	High intensity burn
Gap control		0.79	0.75	0.74
Plant removal			0.82	0.75
Low itensity				0.77
High intensity				

(683° C) and at 3 cm depth (185° C) were well above the temperature range required to kill seeds. Brinkmann and Vieira (1971) found that seeds of 31 Amazon rainforest tree species were killed during fires where soil temperatures at 2 cm depth ranged 95-125° C. Similarly, Uhl *et al.* (1981) reported that seeds of 7 successional species were killed at temperature >100° C. Even the most tolerant hard-seeded species from fire-prone systems are killed at temperatures above 150° C (Probert 1992). Therefore, the few seeds that did survive high-intensity burns likely escaped these high temperatures in unburned patches.

Average soil surface temperatures during low-intensity burns (160° C) were also sufficient to kill seeds. In this treatment, however, the density of viable seed was only reduced by approximately half that of gap controls (15 vs. 32 seeds m^{-2}). This seed survival may reflect the greater heterogeneity of low-intensity burns or it may reflect survival of seeds buried below the soil surface. Average soil temperatures at 3 cm depth during low-intensity burns (54° C) may have been below the range lethal to seeds. Similarly, Uhl *et al.* (1981) found that seed banks were reduced by cutting and burning of Amazonian rainforest, but that a substantial number of buried seeds survived. The number of seeds surviving low-intensity burns may also reflect the resistance of some seeds to low-intensity fires. For example, of 80 *Copaifera chodatiana* seeds placed on the soil surface before low-intensity burns, 35% germinated (Chapter 4).

The high mortality of seeds caused by high-intensity burns implies that seedling regeneration in these plots was mostly limited to seeds dispersed after burns (approximately 24 seeds m^{-2} in the first 9 weeks following burns). Common species establishing after high-intensity burns from seed, *Anadenanthera colubrina, Astronium urundueva,* and *Thiloa paraguariensis,* were species frequently caught in gap seed traps. *Astronium* and *Thiloa* are wind dispersed, and compared with their total seed rain, a disproportionate percentage their seeds were trapped in gaps. This observation agrees with other studies conducted in the neotropics that noted seed rain of wind dispersed seeds is greater in gaps than forest understories (Augsperger and Franson 1988, Loiselle

*et al.*1996). Higher survival of seeds in low-intensity burns implies that seedlings establishing in these plots may have originated either from seed banks or seeds dispersed following burns.

The density of buried seeds in gap control plots (5-164 seeds m^{-2}) was substantially lower than densities reported in the literature for other neotropical forests (344-682 seeds m^{-2} Guevera and Gomez-Pompa 1972, 752 seeds m^{-2} Uhl *et al.* 1981, 177 seeds m^{-2} Uhl *et al.* 1982, 742 seeds m^{-2} Putz 1983, 7000 seeds m^{-2} Young *et al.* 1987, 4535 seeds m^{-2} Butler and Chazdon 1998). The low seed density I observed likely does not reflect an actual difference between the Las Trancas forest and other forest types in seed bank densities, as Vaca (1999) also reported higher seed bank densities in treefall gaps from Las Trancas '95 of 477-774 seeds m^{-2} (sampled to 4 cm depth). This disparity between my results and Vaca's is likely due to difficulties keeping seed flats moist due to a drought that persisted during the first 2 months of my germination trial.

Total plant cover: differences in rates of recovery among treatments

Total plant cover was reduced to zero immediately following burns and plant removal and rates of plant colonization in the following months differed greatly among these treatments. Increase in plant cover was slowest after high-intensity burns, likely due to mortality during burns of both advanced regeneration and seeds stored in the soil. Seeds dispersed in the second year appeared to be an important component of regeneration in high-intensity burn plots; total cover in high-intensity burn plots increased more during the first 6 months of the second year (from 25 to 60%) than during the entire first year (0 to 25%). By comparison, increases in plant cover after low-intensity burns and plant removal were rapid; after only 6 months colonizing plants covered 60% and 75% of these treatments, respectively. Again, the slightly lower cover in the low-intensity burn treatment was likely due to partial sterilization of seed banks and some death of advanced regeneration caused by the burns.

Although canopy cover > 2 m did not differ among gap treatments (Chapter 2), differences in total plant cover < 2 m will create notably different opportunities for establishing tree seedlings.

Due to the abundance of advance regeneration and rapid increase in total cover, gap control plots provide the least suitable establishment sites for new tree seedlings, particularly those of shade-intolerant species. And, although the low-intensity burn and plant removal plots provided ample opportunity for seedling establishment immediately following treatments, this space was re-colonized by competing plants within 6 months. The high-intensity burn treatment provided the most space for the longest period for establishing tree seedlings.

These rapid increases in plant cover stress the importance of early colonization for the successful establishment of tree seedlings. Seedlings that colonized immediately following burns, plant removal, or canopy gap formation would have experienced significantly less competition than those colonizing several months later. The importance of early establishment in determining later success of tree seedlings is frequently reported. For example, Brokaw (1985a) found that growth rates were highest and mortality lowest for trees establishing before or soon after canopy gap formation in Panama.

Dominant life forms and species in gap treatments

Gap treatments altered the relative cover of plant life forms from that of forest understories. For example, shrubs, which were a dominant life form in forest understory plots, formed a low percentage of cover relative to herbs, vines, and trees in all four gap treatments. Also, percent cover of ground bromeliads was lower in the plant removal and burned treatments relative to the forest understory and gap control plots. Within gap treatments, the relative proportions of herb, vine, and tree cover were fairly similar, each contributing approximately 20-30% of total plant cover. Yet within each life form, particular species tended to dominate in different gap treatments.

Herbs. Herb cover in gap control, plant removal, and low-intensity burn plots was dominated by several species in the genus *Ruellia,* perennial herbs in the Acanthaceae. *Ruellia* spp. were the most common germinants in seed banks sampled from these treatments. These species

appear to respond rapidly to canopy opening and/or soil disturbance; while they may persist in forest understories, they form dense hedges along logging roads and skid trails. Also, *Ruellia* was the only genus of any life form that alone covered 100% of some subplots. Due to its tendency to form dense patches, *Ruellia* spp. may be the greatest competitors of establishing tree seedlings in gap control, plant removal, and low-intensity burn treatments.

Ruellia spp. comprised a much smaller fraction of the herb cover of high-intensity burn plots, likely due to seed mortality during burns. Herb cover in high-intensity burn plots after 18 months was largely composed of annual herbs, particularly species of Asteraceae. Although present in the first year following burns, cover of these herbs increased greatly in the second year presumably from newly dispersed seeds. Two other herbaceous species, *Commelina* sp. and an unknown Euphorbiaceae, appeared to establish preferentially in burned areas as well. The distribution of these two species suggest they were present as seeds or bulbs before burns and were stimulated to germinate or sprout by medium or low-intensity heat.

Vines. The dominant woody vine species in the gap control, plant removal, and low-intensity burn treatments was *Mimosa* sp., perhaps more correctly called a scrambling shrub because it is free standing up to heights of 5 m and only then begins to support its limbs on branches of adjacent trees. This species was most frequently the tallest individual in the 4 m² subplots and was the second most common species > 2.5 m tall. In this study, *Mimosa* regenerated exclusively by sprouting from the stem and root collar. These results agree with those of Sampiao *et al.* (1993), who observed higher dominance of *Mimosa* sp. following burns in the Brazilian caatinga, which they attributed to its ability to survive fires by sprouting. It appears that *Mimosa* sp. does not survive fires of high-intensity, as it was infrequent in high-intensity burn plots in my study.

Vine cover in high-intensity burn plots was dominated by a liana species that regenerated primarily from seed, *Thiloa paraguariensis* (Combretaceae). The wind dispersed seeds of *Thiloa*

were the most abundant of any vine species caught in seed traps following burns. Although *Thiloa* did not commonly reach heights > 2.5 m in the treatment plots during the 18 month observation period, it was frequently the tallest individual in high-intensity burn subplots. This species was also abundant in an area of Las Trancas previously burned by a wildfire (Mostacedo *et al.*1999).

Herbaceous vine cover was patchy; where herbaceous vines were present, they tended to dominate all treatments within a block. For example, one block was dominated by two unknown herbaceous vine species (Leguminosae and Euphorbiaceae) and two other blocks were each dominated by *Echinopepon* sp., a herbaceous vine in the Cucurbitaceae. It is noteworthy that herbaceous vines were dominant in only 3 of 16 blocks. Herbaceous vines are often observed proliferating in disturbed forests. For example, in a sub-humid forest in Bolivia, Pinard *et al.* (1998) found a density of 21,000 herbaceous vines per ha the first year following a wildfire. In disturbed dry forest in Ecuador, Gentry (1995) observed that small vines literally blanketed the remaining forest. Other evidence from Las Trancas suggests that vine proliferation in this dry forest may not be as extensive as in other forest sites. Mostacedo *et al.* (1998) found that the sub-humid forest used in the study by Pinard *et al.* (1998) had a greater increase in post-fire vine infestation than an area of Las Trancas damaged by wildfire.

Trees. Although percent tree cover was similar to that of herbs and lianas, the majority of tall individuals were trees. For example, trees comprised 86% of individuals > 2.5 m tall and 53% of the tallest individuals in subplots. Among this group of dominant trees, the majority were non-commercial species. For example, non-commercial species comprised 60% of trees > 2.5 m tall and 70% of the trees that were the tallest individuals in subplots. Most of these non-commercial trees, which are shade tolerant and relatively abundant in forest understories (Killeen *et al.* 1998), regenerated primarily by sprouting from stems present before gap formation. Therefore, where advance regeneration is abundant, regeneration of commercial tree species may be dominated by non-commercial tree species.

This pattern did not occur in high-intensity burn plots. Most advanced regeneration was killed during high-intensity burns, allowing individuals of shade-intolerant commercial tree species to establish and dominate. For example, among the commercial trees > 2.5 m tall and among those tallest in subplots, approximately 50% were located in high-intensity burn plots, the remaining half distributed among the other 3 treatments. Commercial tree species that did dominate in the gap control, plant removal, and low-intensity burn treatments mostly arose from pre-existing stems or roots. For example, *Centrolobium microchaete*, the most common commercial tree species > 2.5 m tall. regenerated as suckers from the root system of mature trees. Tall individuals of *Caesalpinia pluviosa*, a moderately shade-tolerant species, sprouted from cut or broken stems in gap controls. The future value of these sprouting commercial trees is questionable, particularly those sprouting from stems. Due to the susceptibility of cut or damaged stems to fungal pathogens, mature trees that arose as sprouts may not be harvestable. Although root sprouts of temperate species can produce healthy stems (e.g., Blake 1983), little is known about potential value of root sprouts of tropical species.

Bromeliads. Although several bromeliad species are present at this site, only one species, *Pseudoananas saginarius*, is typical of forest understorys. *Pseudoananas* occurs at high densities in Lomerio: approximately 81% of the forest is occupied by these bromeliads and dense patches of roughly 8,000 ramets per hectare may occur (MacDonald *et al.* 1998). Removal of *Pseudoananas* manually or by burning potentially has tremendous consequences on the establishment of other species. In a study specifically addressing the effects of *Pseudoananas* on tree seedling regeneration in Las Trancas, Fredericksen (1998) found that tree seedling establishment and growth was enhanced more by the removal of bromeliads than by the removal of other understory vegetation. Therefore, the rapid colonization witnessed in the plant removal and low-intensity burn treatments may have been in large part due to the removal of *Pseudoananas*.

Dominance of tree and liana sprouts

Tree and liana sprouts were taller, had larger crown areas, larger basal diameters, and more stems than tree and liana seedlings in all gap treatments. Very similar results were reported by Miller and Kaufmann (1998b) who compared the size of tree seedlings and sprouts after slashing and burning of a tropical deciduous forest in Mexico. In their study, they found mean sprout height, crown area, stem diameter, and number of stems were significantly greater than for seedlings.

Miller and Kaufmann (1998b) attributed the larger sizes of sprouts than seedlings to their larger carbohydrate reserves. Sprouts, which draw carbohydrates from pre-established root systems, have much larger carbohydrate reserves than seedlings, which are limited to seed reserves. Even root systems of seedlings may provide larger carbohydrate reserves for sprouting shoots than that provided by seed reserves, particularly in dry forests where most seeds are wind dispersed and necessarily small (Gentry 1995) and root systems are proportionately larger than in wetter forests (Cuevas 1995). In Las Trancas for example, storage tap roots were observed in 3 month-old *Anadenanthera* seedlings.

Sprouts may still have an advantage over seedlings even after both have depleted their carbohydrate reserves. The larger root system of sprouts would offer more surface area for water and nutrient uptake and likely extend deeper into the soil than seedling root systems. This difference would confer an advantage to sprouts, particularly in dry forests where water is seasonally limiting. Root systems of sprouts may also provide an additional source of mineral nutrients for developing shoots. For example, Coutinho (1990) demonstrated that ash contents in the underground organs of woody plants increased and remained elevated for 5 months following ground fires in the Brazilian cerrado.

The high carbon cost of maintaining an extensive root system is one possible disadvantage of sprouts. Sprouts have to export more carbon below-ground to support larger roots systems,

while seedlings with balanced root/shoot ratios may be able to allocate relatively more resources to aboveground photosynthetic tissue. Also, sprouts often divide height growth among multiple stems whereas seedlings usually support only one stem. These reasons may explain why seedlings and sprouts of several tree species had similar relative growth rates during the second year following burns (Chapter 4). Similarly, Miller and Kaufmann (1998b) reported similar relative growth rates among seedlings and sprouts in Mexican dry forest.

Changes in relative dominance of sprouts among treatments

Although sprouts were larger than seedlings in all treatments, the magnitude of this difference was dependent on treatment intensity. For example, while the average height of sprouts was roughly 3 times the average height of seedlings in the unburned treatments, sprouts were only slightly taller than seedlings in the high-intensity burn treatment (Figure 5-6). This general pattern is also apparent for crown area and stem diameter. The shift in relative dominance among sprouts and seedlings in high-intensity burn plots is particularly apparent among individuals > 2.5 m tall. In high-intensity burn plots, seedlings comprised 40% of individuals > 2.5 m tall, whereas in the gap control, plant removal, and low-intensity burn treatments, only 10% of individuals > 2.5 m tall were seedlings.

The decrease in dominance of sprouts in high-intensity burn plots was partly due to lower sprout densities and smaller sprouts in this treatment. Plant cell death during fires depends on both the duration of heating and maximum temperature; fire intensity, therefore, is an important determinate of post-burn sprouting. Often, a greater number of plants of increasingly larger size are killed at higher fire intensities (Moreno and Oechel 1994). Intense fires may also hinder growth of sprouts by killing part of the root system. A decrease in sprout size and density following intense fires has been reported in several studies conducted in tropical forests. For example, Sampaio *et al.* (1993) studied the effects of fire intensity on coppicing of caatinga vegetation in Brazil and found sprouts were both smaller and less abundant in areas that experienced more

intense fires. Similarly, Kaufmann (1991) found decreasing frequency of sprouting and slower sprout growth in areas of greater fire intensity in moist forests in the Brazilian Amazon.

The decrease in dominance of sprouts is also partially due to the greater size of seedlings in high-intensity burn plots. More seedlings reached heights > 2.5 m in high-intensity burn plots than in other treatments. Most of these seedlings > 2.5 m were shade-intolerant species establishing from seeds dispersed after the experimental burns, i.e., *Anadenanthera* and *Astronium*. As discussed in Chapters 3 and 4, relative growth rates of these species were greatest in high-intensity burn plots, presumably due to both increased soil nutrients and decreased competition.

Treatment effects on species richness and composition

Although high-intensity burns caused substantial mortality of advanced regeneration and buried seeds, total species richness in this treatment was higher than in the least disturbed treatment, the gap control. This relatively high species richness in the high-intensity burn treatment was likely due to the presence of several colonizing species that were absent from gap control plots. However, due to the sparse vegetation after high-intensity burns, diversity indices that incorporate abundance of species would likely be much lower in high-intensity burn plots. Therefore, the high species richness found in this study following high-intensity burns should be interpreted with caution. According to the intermediate disturbance hypothesis (Connell 1978) frequent, large, or intense disturbances decrease species diversity. Several studies from tropical forests support this hypothesis. For example, Uhl *et al.* (1988a) found that tree species richness 8 years after abandonment of light-use pastures in the Amazon was relatively high, at 20 tree species per 100 m^2. In contrast, they found that after intense use, pastures recover substantially fewer tree species; they found only 1 tree species per 100 m^2 8 years after abandonment of intensely used pastures. In tropical dry forest in Mexico, Miller and Kaufmann (1998a) similarly observed that

species diversity after slash-and-burn was similar to undisturbed forest, but after 3 successive burns diversity of woody species declined by 25%.

Species composition was in general very similar among gap treatments; similarity indices ranged from 74-82%. The high degree of sprouting may account for this relatively stable species composition. Miller and Kaufman (1998a) attributed the maintenance of diversity following slash-and-burn to the high sprouting capacity of tree species at the Mexican dry forest site. Similarly, in an Australian rain forest, Stocker (1981) observed high floristic stability following felling and burning which he also attributed to the high percentage of trees regenerating by sprouting.

Conclusions

Dominance of species, life forms, and modes of regeneration were all altered by gap treatments. While cover of ground bromeliads and shrubs decreased, cover of trees, herbs, and lianas increased in gap treatments relative to forest plots. Several species also tended to dominate in gap treatments, although species that were dominant in gap control, plant removal, and low-intensity burn treatments differed from species dominant in high-intensity burn treatments. Tree and liana sprouts were the largest individuals in the gap control, plant removal, and low-intensity burn treatments. Seedlings were comparatively more dominant in high-intensity burn plots. Although total species richness was not reduced by high-intensity burns, species composition in this treatment was least similar to gap controls.

Total plant cover increased rapidly in all treatments except after high-intensity burns. Due to this rapid increase, and the abundance of advance regeneration, opportunities for establishing tree seedlings were short-lived in all gap treatments but high-intensity burns. In the gap control, plant removal, and low-intensity burn treatments, commercial trees were dominated by sprouts of non-commercial trees present before gap formation. Only in the high-intensity burn treatment were individuals of commercial tree species dominant. These results have serious implications for silvicultural treatments that aim to improve regeneration from seed of commercial tree species. In

this study, the most intense treatment resulted in the most vigorous regeneration of commercial tree seedlings, yet this treatment also altered community structure and composition more drastically than the other treatments.

CHAPTER 6
COMMERCIAL TREE REGENERATION FOLLOWING
AGRICULTURAL ABANDONMENT
IN BOLIVIAN DRY FORESTS

Introduction

Forest management techniques are strengthened by knowledge of the autoecology of desirable species and knowledge of the forest disturbance regime. Results of the studies presented in Chapters 2-5 indicate that many of the shade-intolerant commercial species in Lomerio require disturbances more intense than canopy gap formation for their regeneration. However, these studies only examined regeneration over an 18-month period. Clearly, knowledge of the autoecology of these species would benefit from studies that examine patterns of regeneration over longer time scales.

In Lomerio, shifting agriculture is the principle occupation of the Chiquitanos and therefore, there is an abundance of fallow agricultural fields abandoned at various times in the past. Examining population structures of individual species in such fields can increase understanding of the regeneration strategies of these species. Furthermore, comparing structural features of secondary forests to mature forests may provide clues to past disturbance regimes or events that structured present-day mature forest.

I examined tree regeneration and stand structure in a 50-year chronosequence of secondary succession after shifting cultivation in Lomerio. My specific objectives were: 1) to characterize population structures of commercially valuable tree species in secondary forests of different ages; 2) to characterize forest structure and diversity in secondary forests of different ages and compare

149

these with mature forest; and, 3) to discuss the role large disturbances may have played in the formation of mature forests in Lomerio.

Methods

Study site and background

The forest fallows chosen for this study were located in lands communally owned by the community of San Lorenzo (Figure 2-1). All fallows were abandoned slash-and-burn agricultural clearings. In Lomerio, forest clearing for slash-and-burn agriculture begins at the beginning of the dry season (May-June), when understories of selected forest are slashed with machetes and then trees are felled by ax or chainsaw. Slash is allowed to dry for at least 2 months until the end of the dry season (August-September), when fields are burned. Fields are not plowed. Crops are planted after the start of the rainy season (October-November). Each field that is opened is used for three to five years, depending on soil fertility. The general sequence of crop rotation for fields on more fertile soils is rice, corn, and occasionally beans the first year, manioc and plantains the second year, corn and rice again in the third year, and manioc or sugar cane the fourth year (McDaniel, unpublished). While the site is being actively farmed, it must be weeded 2-3 times a year to prevent second growth vegetation from taking over. Abandoned fields are sometimes cultivated again after 15-20 years, although many fields are left for much longer periods. The size of agricultural fields varies from 1 to 7 ha, although most fields are about 2 ha (McDaniel, unpublished). Most fields are surrounded by mature forest or older fallows, so seed sources are locally available.

Study plots

Fourteen fallows representing 12 different ages from 1 to 50 years were located with the help of local Chiquitano farmers. Each age had one replicate except for the 1-yr-old fallow, which had 3 replicates. The replicates for the 1-yr-old fallow were used to examine variation among fallows of same age, but were averaged for descriptive statistics. Fallow ages were estimated by

talking with the owners of the original fields. These ages are only estimates and confidence of ages decreases with fallow age. However, I am confident that the chronological order of field abandonment is correct. The mature forest stand used for comparison was Las Trancas '95, the site of the studies described in Chapters 2-5. Data from an intensive floristic inventory conducted in this forest in 1995, prior to the initiation of logging activities, are used for the mature forest values (Killeen *et al.* 1998).

Data collection

Tree inventories were conducted during the wet season (February and March) of 1998. Sampling design follows that of Killeen *et al.* (1998). Within each fallow, six 50x20 m plots were randomly located along transects, with plots separated by 50-100 m. Each plot was composed of nested quadrats, with smaller quadrats situated within larger ones (Figure 6-1). In each quadrat, all trees within the targeted size class were identified to species, their diameter at breast height measured (1.3 m, dbh), and total height estimated visually. In each plot, total plant cover < 2 m and percent cover by lifeform (grasses, herbs, bromeliads, shrubs, lianas, and trees) was estimated visually for four 1 m^2 plots, located at the first established corner. Due to very abundant seed production of *Anadenanthera* the year of this study, newly germinated seedlings of this species were also counted in the 1 m^2 plots rather than the 16 m^2 quadrats in order to distinguish them from seedlings > 1 year-old. Canopy cover was estimated with a spherical densiometer at one corner of each plot. Voucher specimens were collected and identified at the Museo de Historia Natural de Noel Kempff Mercado, Santa Cruz.

Mature forest values of basal area, stem density, and canopy height were obtained from Killeen *et al.* (1998) who sampled 100 plots in a 300 ha area of forest in Las Trancas '95. However, as species richness varies as a function of area sampled, tree species richness was estimated from a subsample of 6 plots randomly selected from Killeen's data set. Plant cover

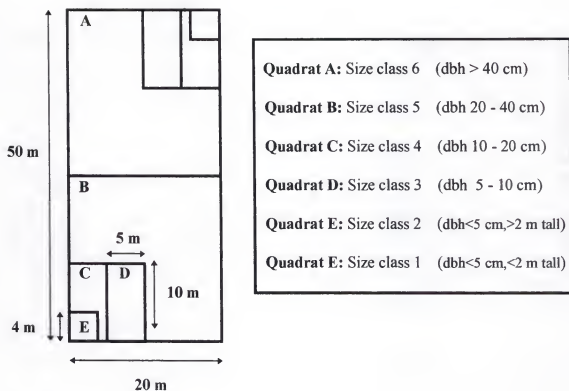|	
Quadrat A: Size class 6	(dbh > 40 cm)
Quadrat B: Size class 5	(dbh 20 - 40 cm)
Quadrat C: Size class 4	(dbh 10 - 20 cm)
Quadrat D: Size class 3	(dbh 5 - 10 cm)
Quadrat E: Size class 2	(dbh<5 cm,>2 m tall)
Quadrat E: Size class 1	(dbh<5 cm,<2 m tall)

Figure 6-1. Layout of sample plots used to measure tree structure and diversity in abandoned shifting agricultural fields. Each plot had nested quadrats of 5 sizes (A-E) with a different tree size class (based on dbh) targeted for each quadrat.

< 2 m and canopy cover of the mature forest were measured in the forest understory plots described in Chapter 2.

Importance values for each species were calculated as the average of relative dominance, relative abundance, and relative frequency. In this chapter, dominance is the proportion of total basal area of each species.

<div align="center">

Results

</div>

Regeneration ecology of selected species

The combined importance values of the commercial tree species listed in Table 6-1 decline with increasing fallow age. In this section, I highlight the population structures of 4 species with the highest total importance values: *Centrolobium microchaete, Anadenanthera colubrina, Astronium urundueva,* and *Acosmium cardenasii.* All four of these species are widely distributed throughout South American dry forests (Prado and Gibbs 1993). All except *Acosmium* are commercially valuable in Bolivia. Additionally, all except *Acosmium* were used in the seed addition treatment of the study described in Chapter 4.

Astronium urundueva **(Figure 6-2).** *Astronium* seedlings were abundant in the 1 and 2-yr-old stands, but scarce in stands >20-yr-old. Population structures in 8-, 20-, 23-, 40-, and 50-yr-old stands resemble an even-aged or single-cohort stand. Density was markedly lower in the mature forest stand than the secondary stands.

Anadenanthera colubrina **(Figure 6-3).** Similar to *Astronium, Anadenanthera* seedlings (> 1-yr-old) and saplings were abundant in young stands, but seedling density (> 1-yr-old) was low in the 15-, 30-, 40-, and 50-yr-old stands. One-year-old *Anadenanthera* seedlings were abundant in all stands; densities ranged from 0.5-22 seedlings m^{-2}. It cannot be stated with certainty that the abundance of the smallest size class in the mature stand was due to 1-yr-old seedlings, as newly germinated seedlings were not distinguished from older seedlings when the mature forest was surveyed in 1995. It is likely this was the case, however, because two years

Table 6-1. Importance values (relative abundance + relative dominance + relative frequency) of individual tree species in each of 12 differently aged stands in a 50-year chronosequence of abandoned agricultural fields. Only species with total importance values for all stand ages greater than 5% are reported. Species are in descending order of summed importance values. Commercial tree species are in bold print.

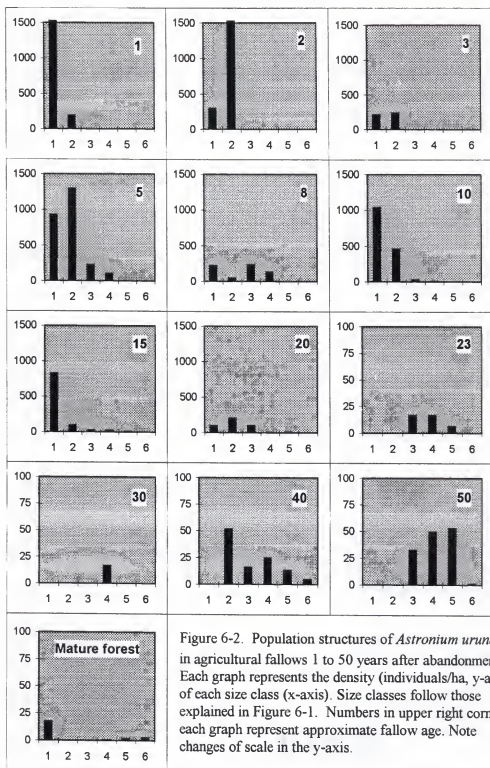| Species	1	2	3	5	7	10	15	20	23	30	40	50	M
Centrolobium microchaete	27	10	32	2	9	1	5	15	24	13	7	4	1
Anadenanthera colubrina	9	8	11	13	11	15	11	7	15	11	11	9	13
Astronium urundueva	9	22	6	18	10	10	8	5	2	1	5	7	2
Acosmium cardenasii	9	1	4	1	5			3	4	6	14	13	30
Phyllostylon rhamnoides	2		2	2	9		2	9	6	6	14	14	1
Casearia gossypiosperma	6	5	2	4	5	3	4	5	4	4	4	3	2
Caesalpinia pluviosa	9	4	3	4	4	5		3	3	2	4	6	3
Cordia alliodora	8	5	7	6	0.4	4	2	3	4	0.5	1	2	0.3
Aspidosperma rigidum	7	2	3	3	1	2	1	2	1		1	3	5
Chorisia speciosa	1					1	3	3	3	8	4	4	2
Machaerium acutifolium	1	2	0.4	2	3		1	1	3	4	4	2	3
Galipea trifoliata	0.4	1		2		2	2	2	2	3	5	4	3
Rhamnidium elaeocarpum	1		4	3	3	1	4	3	5	1			
Simira rubescens	0.4	1	1	2	1	2	2	2	1	5	1	4	1
Allophylus pauciflorius			1	1	7	1	1	4	1	1	3	2	
Spondias mombin	6	5	2	1		1	3	1		1	1	2	1
Guazuma ulmifolia		4	1	4	1	7	2	1	1				
Combretum leprosum				5	2	4	1	4	0.4	2		0	1
Acacia lorentensis	1		1	2	10		1					1	3
Machaerium scleroxylon	0.4		5	1	3	2	1		1	1	1	1	2
Cecropia concolor				2	3	5	5	3		1			0
Bougainvillea modesta				1			2		5	2	4	2	
Cariniana estrellensis			0.4	1		4		1	6			1	
Sterculia apetala			3	1	1		3	1	2	2		1	
Pterogyne nitens			3			2	1	1	2	1	2	2	1
Cedrela fissilis				6		4	1						0.1
Talesia esculenta					1	2	2	2	3	1	1	1	0.1
Neea hermaphrodites							0.3	0.3	1	0.4	1	2	5
Cybistax antisyphilitica	0.3	1	1	2	2	0.4	1		1	1	0.2	1	
Rollinia herzogii			2	1	1	1	2	1				1	
Celtis pubescens				1	2	1	0.5	1	1	1	1	1	0.2
Pogonopus tubulosus			0.4		1		5	1		1			
Eugenia flavescens					0.3		1	2		1	3	1	0.3
Samanea saman				1	1	1	2	1	1	1	1	1	0.1
Enterolobium contortisiliquum					1	1	2	3					0.1
Unknown sp.			1		0.1					0.3	2	1	1
Trema micrantha			5										

Astronium urundueva

Figure 6-2. Population structures of *Astronium urundueva* in agricultural fallows 1 to 50 years after abandonment. Each graph represents the density (individuals/ha, y-axis) of each size class (x-axis). Size classes follow those explained in Figure 6-1. Numbers in upper right corners of each graph represent approximate fallow age. Note changes of scale in the y-axis.
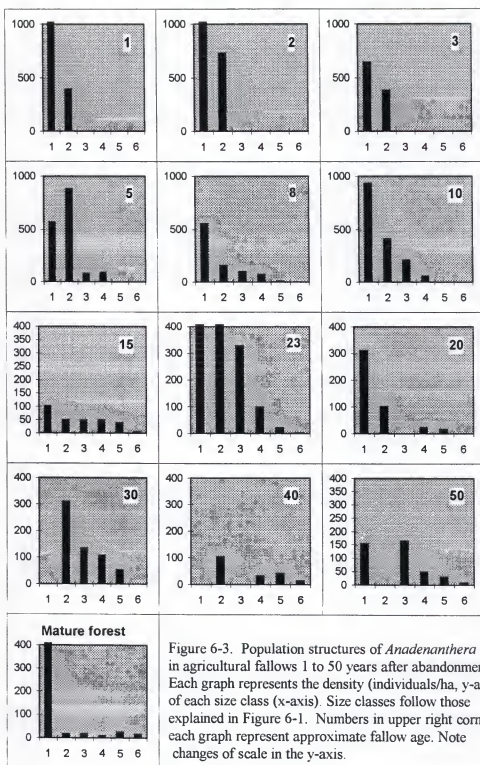
Anadenanthera colubrina

Figure 6-3. Population structures of *Anadenanthera colubrina* in agricultural fallows 1 to 50 years after abandonment. Each graph represents the density (individuals/ha, y-axis) of each size class (x-axis). Size classes follow those explained in Figure 6-1. Numbers in upper right corners of each graph represent approximate fallow age. Note changes of scale in the y-axis.

after the 1995 survey, I did not find a single *Anadenanthera* seedling in 32 plots (4 m^2) sampled in the mature forest understory (Chapter 4). Population structures of the 15-, 40-, and 50-yr-old stands resemble even-aged stands. Excluding the smallest size class (class 1), the population structure in the mature forest also resembles an even-aged stand.

　　　　Centrolobium microchaete (**Figure 6-4**). Patterns in population structures of *Centrolobium* throughout the 50-yr chronosequence are less clear than those of *Anadenanthera* or *Astronium*. *Centrolobium* individuals were more abundant than all other species in the 1-yr-old stand. However, density in older stands was sporadic; fallows ages with small populations (5-, 10-, 15-, 40-, 50-yr-old and mature stands) were interspersed among fallow ages with larger populations (8-, 20-, 23-, 30-yr-old stands). Population structures in the older stands (30-, 40-, 50-yr-old, and mature) appear even-aged.

　　　　Acosmium cardenasii (**Figure 6-5**). The densest seedling bank of *Acosmium* was found in mature forest (7,125 per ha). Although *Acosmium* was established in moderately high densities in the 1-yr-old stand, seedlings were mostly sparse or absent in the 2-, 3-, 5-, 10-, and 15-yr-old stands. Seedlings and saplings were abundant in stands 23-yr-old and older. Population structures in the 30-, 40-, 50-yr-old and mature stands resemble a reverse J-shaped structure

Dominance of regeneration guilds throughout the chronosequence

　　　　Figure 6-6 depicts the dominance of four regeneration guilds (short-lived pioneers, long-lived pioneers, partially shade-tolerant, and shade-tolerant) throughout the 50 yr chronosequence. Classifications are based on species' shade tolerance obtained from Pinard *et al.* (1999). Long-lived pioneers dominate all stands throughout the chronosequence. Shade-tolerant species become more dominant in older stands, but do not dominate long-lived pioneers even in the mature stand. Short-lived pioneers and partially shade-tolerant species did not dominate the successional stands at any point in the chronosequence.
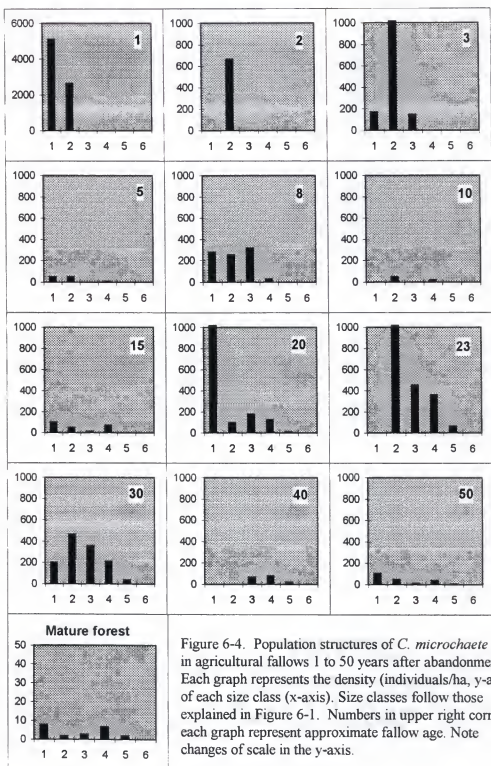
Centrolobium microchaete

Figure 6-4. Population structures of *C. microchaete* in agricultural fallows 1 to 50 years after abandonment. Each graph represents the density (individuals/ha, y-axis) of each size class (x-axis). Size classes follow those explained in Figure 6-1. Numbers in upper right corners of each graph represent approximate fallow age. Note changes of scale in the y-axis.
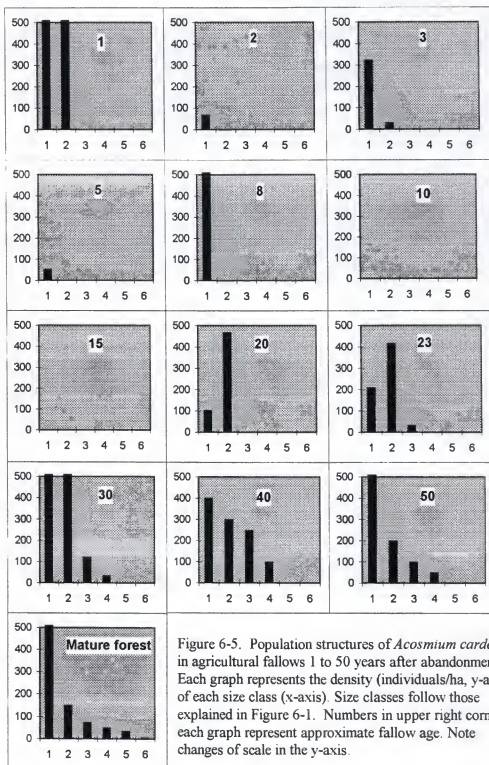
Acosmium cardenasii

Figure 6-5. Population structures of *Acosmium cardenasii* in agricultural fallows 1 to 50 years after abandonment. Each graph represents the density (individuals/ha, y-axis) of each size class (x-axis). Size classes follow those explained in Figure 6-1. Numbers in upper right corners of each graph represent approximate fallow age. Note changes of scale in the y-axis.
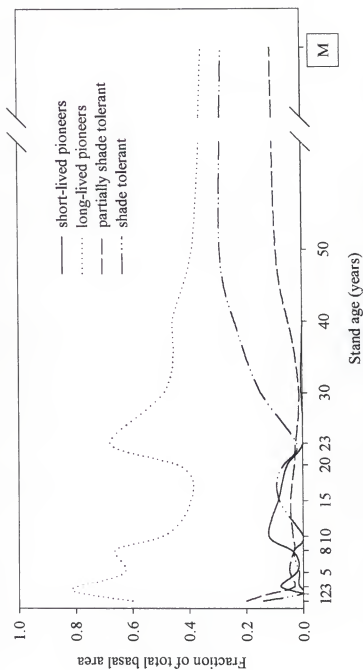
Figure 6-6. Proportion of total basal area of four different regeneration guilds (short-lived pioneers, long-lived pioneers, partially shade-tolerant, and shade-tolerant) over the 50-year chronosequence of forest fallows following agricultural abandonment. Classification of species into regeneration guilds follows Pinard *et al.* 1999. The mature forest is represented by "M."

Species richness and forest structure

Tree species richness reached 75% of mature forest richness within 5 years after agricultural abandonment (Figure 6-7A). Canopy height and basal area were slower to recover; both of these indices were 75% of the mature forest values in the 23-yr-old stand (Figure 6-7B and C). Total stem density (stems > 2 m height) was highly variable in stands up to the 30-yr-old stand (Figure 6-7D); total stem density of the 50-yr-old stand was almost twice that of the mature forest stand.

Changes in stem density and basal area by size class reveal important developments in forest structure (Figure 6-8). Most of the variation in total stem density among stand ages was due to stems < 5 cm DBH; the difference in total stem density between the 50-yr-old stand and mature forest is largely due to the greater abundance of these small stems in the younger stand. In contrast, the variation in total basal area was due more to large stems > 20 cm dbh, reflecting the contribution of large trees. Basal areas of the 5 size classes were similar in the 50-yr-old and mature forest stand, although the mature forest stand had comparatively more basal area in the > 20 cm size classes and less in the < 20 cm size classes.

Canopy cover and understory cover

Canopy cover recovered to 75% of mature forest richness within 8 years after agricultural abandonment (Figure 6-9). Canopy cover of the 50-yr-old stand and the mature forest were similar, both with 80% cover. Grasses and herbs were a dominant part of plant cover in the young stands, but their cover declined in older stands. Shrubs and the common ground bromeliad, *Pseudananas sagenarius*, were absent in young stands but were more abundant in older stands. Tree regeneration lost dominance in the understory in stands >15-yr old, likely due to saplings recruiting into larger size classes. Vine cover varied from 5 to 18% throughout the stands of the chronosequence with no distinct pattern in cover with stand age.
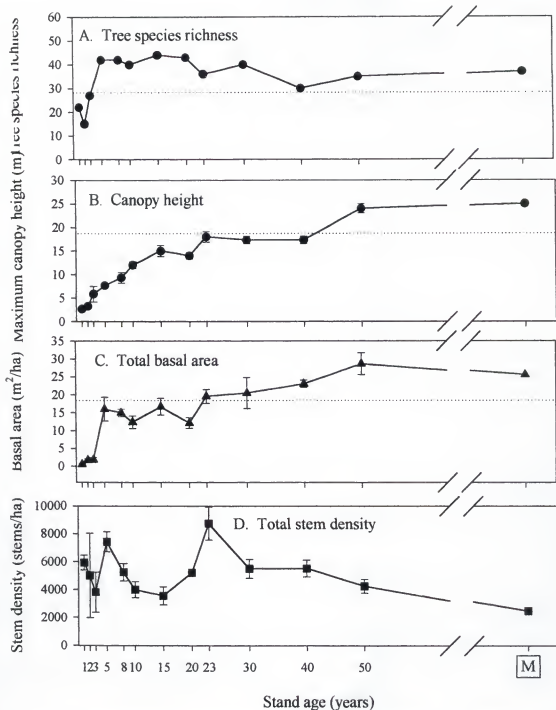
Figure 6-7. Tree species richness, canopy height, total basal area, and total stem density of agricultural fallows 1 to 50 years after abandonment. Dotted lines represent 75% of mature forest values for each index. Tree species richness is the total number of tree species found in each fallow. Canopy height, total basal area, and total stem density are averages (with standard errors) of the 6 sampling plots used in each fallow. Mature forest values are taken from Killeen *et al.* (1998). Stem density does not include stems < 2 m tall.
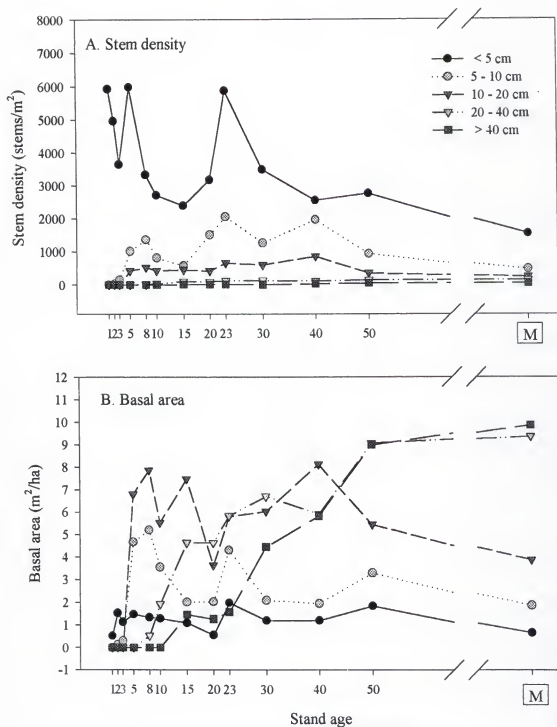
Figure 6-8. Stem density (A) and basal area (B) by diameter size class of agricultural fallows 1 to 50 years after abandonment. The mature forest stand is designated on the x-axis by a "M".
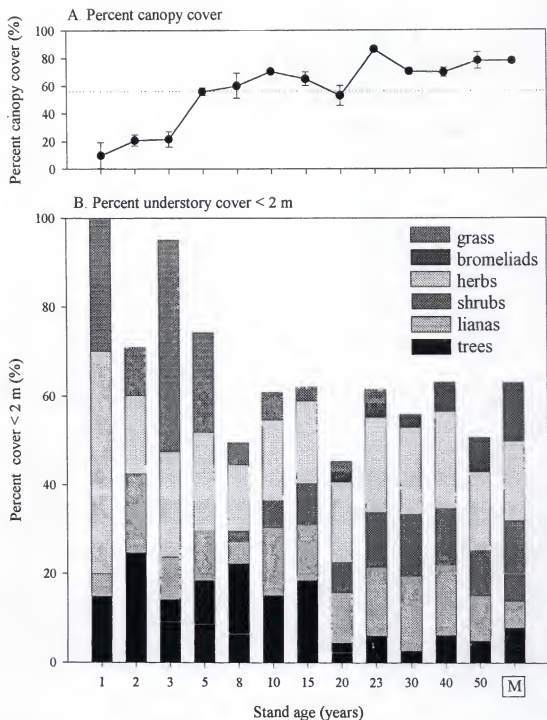
Figure 6-9. A. Percent canopy cover > 1.3 m measured with a spherical densiometer, and B. percent understory cover <2 m by lifeform. The mature forest stand is designated on the x-axis by a "M".

Discussion

Tree species regeneration strategies

The four species I have highlighted show considerable variation in their regeneration strategies. Based on their size-class distributions in the chronosequence as well as results from experimental studies (Chapter 4 and 5), these species span the continuum from shade-intolerant to shade-tolerant. *Acosmium*, with its densest seedling bank in mature forest, appears to regenerate well in the shade and is the most shade-tolerant of the four species. The remaining three species all exhibit characteristics of shade-intolerant regeneration, but appear to require different degrees of disturbance for their regeneration.

Of the four species, *Astronium* is perhaps the most shade-intolerant. Based on the absence of seedlings in older fallows, *Astronium* appears to have little ability to establish in shade. However, canopy opening alone does not appear to be sufficient for its regeneration. Even with seed addition, *Astronium* seedlings did not establish under canopy gaps, but did establish following plant removal and controlled burns (Chapter 4), suggesting this species may need soil disturbance for its establishment.

Unlike *Astonium*, *Anadenanthera* has the ability to establish in forest understories; newly germinated seedlings were abundant in all stands in the chronosequence. However, this seedling bank appears to be emphemeral. Mortality of *Anadenanthera* seedlings in forest understories was high (Chapter 4) and few are expected to recruit into larger size classes. The low density of individuals in the second size class in the mature stand supports this claim. Therefore, *Anadenanthera* appears to be less shade-intolerant than *Astronium* because it can establish in shade, but still requires disturbance to survive beyond the seedling stage and recruit into larger size classes.

The sporadic abundance of *Centrolobium* among the differently aged stands may be due, in part, to its mode of regeneration. *Centrolobium* primarily regenerates vegetatively as root

sprouts from the root systems of mature individuals (Chapter 4 and 5); *Centrolobium* seeds have extremely low viability. This mode of regeneration would contribute to a clumped distribution, as regeneration would be more abundant near mature individuals. A clumped distribution would explain why *Centrolobium* was abundant in some fields and almost absent in others. Rather than light availability alone, *Centrolobium* may be dependent on damage to a mature individual for regeneration.

Despite their different regeneration strategies, *Anadenanthera*, *Astronium*, and *Centrolobium* can be classified as long-lived pioneers (Finegan 1996); they all exhibited shade-intolerant regeneration, become emergents at maturity, and produce dense wood (1.00, 1.10, and 0.75 g/cm^3, respectively). Approximately 13 commerical species in Lomerio also show characteristics of long-lived pioneers. As with *Anadenanthera*, *Astronium*, and *Centrolobium*, these other shade-intolerant commercial species were more dominant in forest fallows than the mature stand. Although long-lived pioneers dominated all successional stands, with increasing stand age their dominance declined as that of more shade-tolerant species increased. Without introducing new disturbance to the mature stand, populations of long-lived pioneers will senesce, and the abundance of shade-intolerant commercial species will likely decline.

Successional patterns and recovery of forest structure

The patterns of change in forest structure observed among the variously aged abandoned fields in this study follow descriptions of tropical secondary forest dynamics reviewed by Brown and Lugo (1990), specifically, total stem density decreases during stand development as density of trees >10 cm dbh, canopy height, and basal area increase. These structural changes occurred relatively quickly in this chronosequence: tree species richness reached 75% of mature forest richness in the 5-yr-old stand and both basal area and maximum canopy height reached 75% that of mature forest in the 23-yr-old stand.

These rates of recovery relative to mature forest values are among the higher rates documented in other studies of tropical forest regeneration, particularly for species richness (Table 6-2). It is important to note, however, that species richness and species composition vary independently, and although many studies report quick recoveries of species richness, species composition is almost always slower to recover (Finegan 1996).

The fast relative recovery of the Bolivian site compared to the other forest sites may be due to several factors. First, a high percentage of tree species in these forests regenerate by sprouting. Communities with a high percentage of sprouting species are thought to be more resilient to disturbance (Janzen 1975, Ewel 1980, Cortlett 1981, Nyerges 1989), as growth rates of sprouts are generally higher than that of seedlings, allowing sprouts to form taller and larger crowns soon after disturbance (Miller and Kauffman 1998b, Chapters 4 and 5). And, although not quantified, seed rain of trees into abandoned fields was potentially high due to the large percentage of wind dispersed tree species in this forest (Justiniano 1997) and the relatively small size of forest clearings (usually ~2 ha).

Notably, short-lived pioneers did not dominate the successional stands early in the chronosequence (Figure 6-6). Instead, long-lived pioneers begin to dominate the stands almost immediately. This pattern contrasts with succession in tropical moist forests, where short-lived pioneers typically dominate successional stands for up to 10 years (Uhl *et al.* 1981, Finegan 1996, Howlett 1998). This pattern may be related to differences among dry and moist forest tree species in the ability of their seeds to establish and survive in abandoned fields. As Anderson (1990) explains, the microclimatic gradient from forested to non-forested sites is notably steep in the moist tropics. This gradient is more gradual in dry forests, due to a more open mature forest canopy. Therefore, while many species common in mature dry forests are adapted to growing in high light conditions, non-forested sites may be beyond the physiological tolerance of many forest trees in the moist tropics (Anderson 1990).

Table 6-2. Comparison of rates of recovery of basal area, tree species richness, and canopy height reported by other studies of forest succession in the tropics and subtropics. For each index, the age by which secondary stands reach 75% of the mature forest stand and the mature stand values are reported.

Forest type	Basal area (m²/ha)		Canopy height		Tree species richness		Source
	Age @ 75%	Mature (m²/ha)	Age @ 75%	Mature (m)	Age @ 75%	Mature (#)	
montane	>>30	60.3	>>30	36	15	20	Kappelle et al. 1996
lower montane	>35	62.8	11	21	>35	105[a]	Kuzee et al. 1994
subtropical wet	20	33.8	20	24	>21	37	Lugo 1990
subtropical wet					25	20	Aide et al. 1995
tropical moist	> 80	34.8	>35	25-35	60	67	Saldariagga et al. 1986
tropical moist	> 80	35.6			5	66	Saldariagga et al. 1988
tropical wet					>17	70	Guariguata et al. 1997
tropical wet	17	33	>10	10.4	10	25	Aweto 1981 a, b
tropical dry	23	25	23	25	5	37	This study

>> signifies that the mature stand value was more than twice that of the oldest secondary stand reported.

[a] Total species richness

While it is likely that differences in climate or soil fertility may be partly responsible for the differences in regeneration rates among the forests types listed in Table 6-2 (Lugo and Brown 1990, Guariguata *et al.*1997), the type and intensity of previous use also influences rate of recovery. For example, Aide *et al.* (1995) found forest growth to be much slower after pasture abandonment than following less intense forms of disturbance in wet forests of Puerto Rico. In Mexican humid forests, above-ground biomass accumulation was inversely related to the duration of prior land use (Hughes et al 1999). Kappelle *et al.* (1996) found less abundant oak regeneration in areas of Costa Rican montane forest that had experienced high-intensity burns. In the Venezuelan Amazon, tree species richness was 3 to 66 times greater in land that was immediately abandoned after slash-and-burn than land that was cultivated before abandonment (Uhl *et al.*1988a). Therefore, the rates of recovery of these different forests should be interpreted with caution, as the intensity of disturbance likely differed among the studies.

Although a distinct pattern emerged from the chronosequence, there was notable variation in structural traits among the different stands not explained by differences in age. For example, the 23-yr-old stand had higher stem densities and canopy height than expected. This may be due to a number of factors that likely varied between fields formed at different times and in different locations, including differences in the length of cultivation, soil type, size of clearing, availability of propagules, and rainfall during the first years of development, or disturbance by fire, cattle grazing, or fuel wood collection in the years after abandonment. Substantial differences among the three stands formed in the same year suggest that variation among factors operating very early in succession, such as initial site conditions, seed dispersal, germination, and predation, could account for much of the variation among stands. The three 1-yr-old stands had ranges of tree species richness of 11-18 species, basal area 0.84-2.28 m^2/ha, and stem density of 9,880-42,800 stems/ha < 5 cm dbh.

History of the mature stand

The dominance of long-lived pioneers and their even-aged size class structures in the mature stand indicate the present forest formed after a severe disturbance. Several additional findings suggest that this disturbance was most likely fire. Dendrochronology of *Cedrela fisilis*, one of the few species that creates annual rings, indicated that intense fires have occurred roughly every 30-60 years in Las Trancas (J. Huffman, pers. comm). In the course of the soil studies conducted in Chapter 3, I found charcoal fragments at various locations and soil depths in both Las Trancas '94 and '95. Although the cause of these past fires are unknown, pottery shards (found in soil sampled from 6 different sites within Las Trancas) suggests that at least some fires were anthropogenic in origin.

How old is the "mature forest?" While this stand's structural features such as stem density and total basal area are very similar to those of the 50-yr-old stand (Figure 6-8), more information on features that may change less dramatically, such as the composition of understory species or size of the largest individuals, may show that it is much older. For example, the largest tree in the mature stand was 115 cm dbh (*Schinopsis brasilensis*), in the 50-yr-old stand it was only 78 cm dbh (*Phyllostylon rhamnoides*). Presumably, the mature stand is as old as its even-aged population of canopy trees. According to estimates from other neotropical forests, the life-span of long-lived pioneers ranges from 75 to 150 years (Lieberman and Lieberman 1987, Finegan 1996).

The role of disturbances in the dry forests of Lomerio

There is ample evidence that disturbance, of both natural and anthropogenic origins, has been an extensive force throughout the Amazon basin for millenia (Clark and Uhl 1987, Goldammer 1990, 1992, 1993, Schule 1990, Kershaw 1997). Much of what was once considered virgin forest is now recognized as regrowth (e.g., Budowski 1965, Denevan 1976, Denevan et al. 1989). This study provides additional evidence of the pervasive, if not frequent, role of

disturbance in the neotropics. And, I will argue that, tropical dry forests have likely been more prone to both natural and human disturbance than wetter regions of the Amazon basin.

Previously, major fires were thought to occur infrequently in tropical dry forests (Malaisse 1978, Janzen 1988, Murphy and Lugo 1986) presumably due to the sparcity of combustible material on forest floors (Hopkins 1983). However, natural fires caused by dry thunderstorms are likely to occur during the transition from the dry period to the rainy season, and have been witnessed in dry tropical forests (Middleton *et al.* 1997). The susceptibility of this vegetation type to natural fire is also supported by the charcoal record. Radiocarbon dates of charcoal throughout the Amazon correspond to dry episodes during glacial periods when dry forests expanded and more humid forests contracted (Goldhammer 1993, Clark and Uhl 1987, Saldriagga *et al.* 1986). Janzen (1975) hypothesized that the dominance of sprouting species in the dry tropics, as well as the comparatively simple forest structure, may be the consequence of their more extensive disturbance regime. Evidence from lowland Bolivia suggests that dry forests suffered less mortality from wildfire than moister forests (Mostacedo *et al.* 1998), which may also be indicative of the pervasive role fires have played in dry forests.

In the dry forests of Bolivia, anthropogenic disturbance also has likely been more extensive than in wetter parts of the Amazon. Denevan (1976) estimated that the pre-European contact population density of the region that includes Chiquitania was nine times higher than other Amazonian lowland forests, due to its more fertile soil. In fact, present population densities in Lomerio (~2.0 people km^{-2}) are only slightly higher than the pre-contact density estimated by Denevan (0.6-1.8 people km^{-2}). Indicative of this high indigenous population, Chiquitania was one of the centers of Jesuit missions in South America. Within Chiquitania, Lomerio has historically been a refuge of indigenous people fleeing the Jesuit missions in the 1700s, and later, white land owners and rubber barons attempting to enslave them in the 1800s and early 1900s (Krekeler

1985). The even-aged population structure of many of the shade-intolerant tree species may in fact be the legacy of centuries of slash-and-burn cultivation.

Implications: Management potential of secondary forests in Lomerio

Management potential of any forest stand is dependent on the harvestable volume of trees. In Lomerio, approximately half of the commercial timber tree species are long-lived pioneers and are found in abundance in secondary forests. The 50-yr-old stand in this study averaged 30 commercial trees of harvestable size (> 40 cm DBH) per hectare, comparable to the number in mature forest (33 trees/ha).

The abundance of shade-intolerant commercial tree species in secondary forests and the decline in their populations in maturing stands has important implications for the future management of these species in Lomerio. Managing secondary forests for secondary forest species (i.e., long-lived pioneers) is likely a more viable strategy than the current practice in Lomerio: managing mature forests for secondary forest species. Managing mature forests for species that naturally regenerate in even-aged populations logically entails heavy intervention (Dawkins 1958). As such, silvicultural methods intensive enough to enhance regeneration of long-lived pioneers are also likely be very expensive. In Bolivia, preliminary cost estimates of using prescribed burns to enhance regeneration of the species highlighted in this study were higher than the expected benefits resulting from increased seedling densities ($8-14 per gap; Ramirez, 1998). Use of secondary forests in Lomerio could offset these high silvicultural costs by taking advantage of the abundant regeneration of commercial species in agricultural fallows.

Additionally, intensive silvicultural treatments may compromise goals of maintaining forest integrity and biodiversity. In Lomerio, the objective of the current management plan is to sustainably produce timber while minimizing negative impacts on the other biological and physical resources in the forest (Pinard *et al.* 1999). Although the dry forests in Lomerio may be more

resilient to disturbance than wetter tropical forests, intensive silvicultural intervention (i.e.,
prescribed burning) may alter species composition if applied on a large scale (Chapter 5).

Management of secondary forests for timber is certainly not a new idea (e.g., Holdridge
1957, Ewel 1979, Wadsworth 1983, Budowski 1985, Lamprecht 1989, Dubois 1990, Finegan
1992). High concentrations of economically important tree species (i.e., *Didymopanax*, *Vochysia*,
Cordia, *Simarouba*, *Goupia*, *Laetia*, *Cedrela*) have been documented elsewhere in secondary
neotropical forests (reviewed by Finegan 1992). In fact, one of the earliest tropical silviculture
systems was based on the management potential of abandoned slash-and-burn fields. Developed
by Dutch foresters in Burma in the mid 1800s, the *taungya* or *tumpang sari* system "leased" royal
forest lands to shifting cultivators who planted teak between their usual crops of rice and cotton.
After several years of cultivation, fields were left fallow and managed for teak (Peluso 1992,
Palmer and Dawkins 1993, Dawkins and Philip 1999). A more recent example is the Trinidad
Shelterwood system, initiated in the 1950s, in which secondary forests in Trinidad were managed
for fast-growing, light-demanding species such as *Didymopanax*, *Byronsomium*, and *Laetia*
(Finegan 1992).

The management of secondary forest in generally is only economically possible where the
light demanding trees are commercial as opposed to merely utilizable (Finegan 1992); this
condition which exists in Bolivia (Tabel 1-1). However, use of secondary forests in Lomerio
would not prevent harvesting of mature forest altogether. There was a notable lack of shade-
tolerant species in secondary stands, and therefore a lower diversity of commercial species. In
order to maintain current markets for these species, it would be necessary to manage mature forest
for shade-tolerant species. The silvicultural treatments required to insure the regeneration of
shade-tolerant species in mature forest require comparatively little intervention and are therefore
not likely to be as costly or detrimental to biodiversity.

CHAPTER 6
SUMMARY AND CONCLUSIONS

Summary of Study Results

Due to the diversity of regeneration strategies among commercial tree species in Lomerio, canopy gap formation, plant removal, and low and high intensity controlled burns had variable effects on their regeneration.

Regeneration of shade-intolerant species that lacked seedling banks was dependent on the creation of sites suitable for their seedling establishment, growth, and survival. Reduction of competing vegetation by controlled burning and plant removal benefited seedling establishment of shade-intolerant species. Subsequent seedling survival and growth of these species was greatest after high intensity burns, likely due to the slow recovery of competing vegetation and the dramatic, although short-lived, increase in available nutrients.

Shade-tolerant species had seedling banks in mature forest understories, therefore the success of these species was dependent on the survival of this advanced regeneration and the creation of microsites that enhanced growth. Although survival of advanced regeneration was high in canopy gaps, growth of this regeneration will likely be slow due to the abundance of competing vegetation. Sprouting of shade-tolerant species was a common means of surviving plant removal and low intensity burns. Sprouts exhibited vigorous growth and dominated con-specific seedlings in these treatments. Most advanced regeneration of shade-tolerant species was killed during high intensity burns.

At least one commercial tree species in Lomerio regenerates predominately as root sprouts. Root sprouts of this species, *Centrolobium microchaete*, were most abundant in gaps

where a mature individual was harvested. Within these gaps, root sprouts were most abundant in treatments where damage, but not mortality, of roots was likely (plant removal and low intensity burn treatments).

Overall, sprouting proved to be an important pathway for regeneration following treatments. Sprouts, from roots, root collars, or stems, dominated canopy gap, plant removal, and low intensity burn treatment plots throughout the study. In treatment plots not dominated by root sprouts of *Centrolobium microchaete*, the largest sprouts were of non-commercial species. Commercial tree seedlings were among the largest individuals only on high intensity burn plots. The importance of sprouting in this dry forest likely contributed to a relatively high species similarity among treatments. Only where the frequency of sprouting was reduced by high intensity burns, was species composition altered most from the other treatment plots.

Regeneration of shade-intolerant tree species was also abundant in recently-abandoned slash-and-burn fallows in Lomerio. Older fallows (40-50 yrs) had similar densities of commercial trees as managed mature forest. The mostly even-aged stands of shade-intolerant canopy species in the mature forest suggest that it developed after some type of large-scale disturbance. Pottery shards and charcoal fragments found in soil sampled from this mature forest suggests it may have once been under cultivation.

Implications for management

In Lomerio, tree species spanning the continuum from shade-intolerant to shade-tolerant are commercially valuable and are harvested from mature forests. Due to the well-planned, labor intensive harvesting operations and the relatively low volume of timber extracted, only modest disturbance to the remaining forest occurs. This management scheme may be suitable for one group of commercial species: shade-tolerant species that may only require small canopy openings to release their advanced regeneration. As is commonly recommended for managed natural forests in the tropics, managing advance-regenerating species would require little damage to the

residual forest during harvesting operations, as apparently is happening in the managed forests of Lomerio. Due to the abundance and vigor of competing vegetation in harvesting gaps, additional treatments such as weeding, release, or thinning may be necessary at various intervals after harvesting. Alternatively, limiting the sizes of harvesting gaps to discourage dense regeneration of more light demanding non-commercial species may also aid the growth and survival of advanced-regeneration of commercial species.

In contrast, harvesting activities alone do not provide appropriate microsites for the regeneration of many commercial species in Lomerio, the majority of which are shade-intolerant. Most of these species lack seedling banks in mature forests and therefore must rely on regeneration from seed following harvest. The results of these studies suggest that even large, multiple-tree harvesting gaps do not provide sufficient light for seedling establishment of many of these species, again due to the abundance of competing vegetation. By reducing this competition, exposing mineral soils, and increasing available forms of nutrients, controlled burns can enhance seedling establishment, growth, and survival of these shade-intolerant species. Although this evidence strengthens the promise of controlled burns as a silvicultural tool in Lomerio, several points still need to be addressed before burns should be prescribed on a management scale.

Fire intensity. Controlled burns can be manipulated in various ways to achieve different results. The "success" of controlled burns depends to a great extent on if their results meet specified management objectives. Fire intensity is an important determinate of the extent and duration of competition removal, the amount of mineral soil exposed, and alterations of nutrient availability. While low intensity burns control competing vegetation little more than manual plant removal, high intensity burns prevent regeneration of all but the most fire-tolerant sprouting species or those colonizing from dispersed seeds. Also, high intensity burns can greatly increase available nutrients, but often at the expense of total nutrient stores and soil structure. Low intensity burns increase available nutrients to a lesser extent than high intensity burns, but also are not as

damaging to soil physical properties. Forest managers should control, as much as is possible, the intensity of burns in accordance with their management objectives.

Seed availability. Improving microsite conditions for establishment of shade-intolerant species through controlled burning will only meet management objectives if seeds are available. Due to the irregular inter-annual reproduction of many of tree species in Lomerio, seed limitation will likely be a problem for at least some commercial species in any given year. Also, seed trees of most commercial species are infrequent, and therefore, their seeds are patchily dispersed. Therefore, augmenting naturally dispersed seeds should be done in combination with controlled burns to ensure sufficient seedling establishment. Although low seed longevity may prevent seed storage from year to year, manually redistributing collected seeds into burned areas should increase seedling abundance of many species. Also, as few seeds on soil surfaces or buried in the soil survive burns, the timing of burns can also be controlled to maximize seed availability. Seed survival is most easily ensured by timing controlled burns before peak seed fall of targeted commercial species.

Deciding when and where controlled burns are appropriate. Intensive silvicultural treatments such as controlled burns designed to enhance regeneration of shade-intolerant species will also damage or kill advanced regeneration of shade-tolerant species. This conflict requires that species guilds be managed either in different areas or at different times. For example, if advanced regeneration of shade-tolerant species is sufficient in forest understories, then low impact harvesting methods followed by weeding or thinning should be prescribed rather than more intensive treatments such as controlled burns.

Alternatively, these two guilds can be managed within the same forest at different cutting cycles, as in the Trinidad Shelterwood System (Finegan 1992). The TSS was projected as a polycyclic system with a 60-year rotation and two 30-year cutting cycles. The first harvest focused on the even-aged stand of fast growing shade-intolerant species and the second harvest

was to have exploited the more shade-tolerant species which regenerated continuously in the understory. In order to maintain current markets for Bolivian timber species, management units should be at different cycles in the rotation to ensure supplies of both secondary and more shade-tolerant species. However, even in this polycylic system, the choice of opting for intensive silvicultural treatments over less intensive treatments will still arise at the start of each new rotation.

A second alternative is to reserve management of mature forests for more shade-tolerant species while focusing management of shade-intolerant species where their regeneration is abundant, such as in secondary forests that regenerate following abandonment of slash-and-burn fields. Commercial management of agricultural fallows for shade intolerant species was a common practice in Burma in the late 1800s and early 1900s (Dawkins and Philip 1998) and more recently has been attempted with promising results in Mexico (L. Snook, pers. comm.). One advantage of harvesting shade-intolerant species from abandoned slash-and-burn fields is that the costs of these intensive silvicultural treatments are incorporated into the traditional agriculture system of the local population. However, this system has several disadvantages, including the small size of clearing made by farmers, as well as maintaining fallows for longer rotation periods than local farmers are accustomed. Also, farmers may not wish to travel far from their communities causing difficulties in the distribution of harvest units over the entire forest.

Gaps in knowledge of controlled burns in managed tropical dry forests

Effects of scale. Although many of the changes brought about by burns are short lived (e.g., nutrient availability), other changes may last for longer periods (e.g., altered soil physical properties). This study examines only a short duration of forest regeneration following controlled burns. Furthermore, the controlled burns in this study were small in scale. As area:edge ratios are likely to affect regeneration (i.e., through their affects on dispersal, predation, duration of insolation, etc.), the effects of controlled burns are expected to vary with burn size. As such, the

ecological effects of larger burns, as well as long-term effects of small and large burns, should be documented to provide a more complete knowledge base for forest managers.

Economic viability. The studies presented in this dissertation only document ecological effects of controlled burning. Before burns are prescribed on a management scale, the economic viability of controlled burning in Bolivian forests should be assessed as well. Preliminary costs estimates by BOLFOR suggest that, due to the labor needed to construct fire breaks and guard burns, burning relatively small areas such as harvesting gaps is not cost-effective. Burning large areas may be more cost-effective, as cost per unit area decreases with increasing burn size. However, conducting large burns requires considerably more skill and knowledge of fire behavior than smaller burns, and therefore education and training of burn crews will become more important, and possibly more expensive.

Interpretations of any economic analysis must be based on what factors are accounted for in the analysis. According to some authors, present investments in silvicultural treatments for a tree crop that will be harvested in 30 years are likely to be financially unattractive due to the high discount rates typical of many tropical countries (e.g., Rice et al. 1997). However, this argument is based on no consideration of externalities (i.e., costs to biodiversity, watersheds, air quality, etc.). Improving regeneration through controlled burns may indirectly benefit the conservation of biodiversity and maintain water and air quality by slowing the conversion of managed forests to non-forest uses. On the other hand, controlled burns may also alter biodiversity as well as lower air and water quality through the release of particulates.

Economic analyses of prescribed burning will also be complicated by the contribution of prescribed burns to carbon emissions. The potential for carbon release from forest fires can be magnitudes greater than that caused by logging (Nepstad et al. 1999), therefore carbon emissions from prescribed burns should be accounted for in economic analyses where externalities are considered. The danger of fire escapes from prescribed burns, and the resulting carbon emissions,

are potentially costly as well. For example, in the dry season of 1999, wildfire damaged over 1.6 million hectares of Bolivian forests, liberating an estimated 17.3 million tons of carbon into the atmosphere (W. Cordero, pers. comm.). This estimate of carbon emissions, from only one wildfire season, is roughly equivalent to the 30-year goal for carbon sequestration of a 2.1 million hectare addition to the Noel Kempff Mercado National Park in eastern Bolivia, a purchase that was funded through a carbon-offset program (Environmental News Network 1998). Although introducing more fire into a system through prescribed burning may be viewed as increasing the danger of fire escape, sound fire management can actually decrease the likelihood of wildfire.

Fire management policy. If controlled burning is adopted as a forest management tool in Bolivia, it should be as a part of a larger integrated fire management system. In addition to using controlled burns to meet management goals, integrated fire management requires the capability to actively manage all fire situations, including preventing and/or suppressing undesirable fires (Goldammer 1992). In addition to the relevant ecological and economic knowledge, an integrated fire management system requires substantial infrastructure and trained personnel. Many Bolivian forest managers express a doubt that fire management will be conducted in Bolivian forests in the near future, citing the inaccessibility of forests and the weak institutional capacity of organizations that might eventually conduct fire management as two important barriers to implementation (K. Gould, pers. comm.).

Although the studies described in this dissertation suggest that controlled burns may benefit the regeneration of commercial trees in Bolivian dry forests, it is likely that institutional and economic factors will ultimately determine whether prescribed burning is integrated into forest management.

Appendix. Species recorded in four gap treatments 9 months following burns. The frequency of each species in the 16 plots of each treatment is listed for gap controls (GC), plant removal (PR), low intensity burn (LI) and high intensity burn (HI). "ALL" is the frequency of species in all 64 treatment plots.

Family	Species	Frequency per treatment (%)				
		GC	PR	LI	HI	All
Bromeliads						
Bromeliaceae	*Psuedoananas saginarius* (Arruda)	100	100	100	69	92
Cacti						
Cactaceae	*Pereskia sacharosa* Griseb.					
Cactaceae	*Cereus tacuaralensis* Cardenas	6	6	6		5
Cactaceae	*Opuntia brasiliensis* (Willd.)	31	19	6		14
Fern						
Schizeaeceae	*Anemia rotundifolia* Schrader	25	19	13		14
Grass						
Cyperaceae	*Cyperus sp.*		19	13	13	11
Poaceae	*Chusquea ramosissima* Lindm.	6	6			3
Poaceae	*Panicum sp.*	6	6	19		8
Poaceae	*Lasiacis sorgoides* (Desv.) Hitchc.	19	31	31	25	27
Poaceae	*Olyza latifolia* Desv.	44	31	19	19	28
Poaceae	Poaceae sp. 1	19	19	25	19	20
Poaceae	*Pharus lappulaceus* Aubl.	56	50	31	13	38
Poaceae	Poaceae sp. 2	19	13	25	25	20
herb						
Acanthaceae	*Anisacanthus boliviensis* (Wees.)		6		6	3
Acanthaceae	*Justicia velascana* Lindau			6		2
Acanthaceae	*Ruellia brevifolia* (Pohl)	6				2
Acanthaceae	*Ruellia sp. 1*	88	94	88	50	80
Acanthaceae	*Ruellia sp. 2*	88	94	88	31	75
Acanthaceae	*Ruellia sp. 3*	50	50	56	13	42
Acanthaceae	*Ruellia sp. 4*	75	88	88	38	72
Amaranthaceae	*Chamissoa acuminata* Mart.	6	13	6		6
Amaranthaceae	*Iresine diffusa* H.& B. ex Willd.	25	6	19	6	14
Araceae	*Anthurium plowmanni* Croat	6	25	13		11
Araceae	*Anthurium sp.*			6		2
Araceae	*Philodendron camposportoanum* G.M. Burrose	19	13	13	13	14
Araceae	*Philodendron tweedieanum* Schott	88	69	75	31	66
Asteraceae	*Ageratum sp.*		38	50	31	30
Asteraceae	Aster sp. 1		6			2
Asteraceae	Aster sp. 2		6			2
Asteraceae	Aster sp. 3		6			2
Asteraceae	Aster sp. 4				6	2
Asteraceae	Aster sp. 5		6	6	13	6

Appendix A. (continued)

Family	Species	Frequency (%)				
		GC	PR	LI	HI	All
Asteraceae	Aster sp. 6			19	50	17
Asteraceae	*Chromolaena extensa*	19	13		6	9
Asteraceae	*Erechtites hieracifolia*				6	2
Commelinaceae	*Commelina sp. 1*	38	44	38	38	39
Commelinaceae	*Commelina sp. 2*	13		6	6	6
Commelinaceae	*Commelina sp. 3*	19	31	38	38	31
Commelinaceae	*Commelina sp. 4*					
Commelinaceae	*Dichorisandra sp.*	6			6	3
Costaceae	*Costus arabicus* L.	31	25	38	19	28
Euphorbiaceae	*Acalypha multicaulis* Mull.	56	75	81	50	66
Euphorbiaceae	*Croton sp.*	6	13	6	13	9
Euphorbiaceae	*Manihot sp. 1*	6	6			3
Euphorbiaceae	*Manihot sp. 2*	6	13	19	13	13
Euphorbiaceae	*Manihot sp. 3*					
Euphorbiaceae	*Sebastiana sp.*				6	2
Euphorbiaceae	Euphorb sp.1	38	19	25	38	30
Euphorbiaceae	Euphorb sp.2	13	13	6		8
Leguminosae	Legume sp. 1			6		2
Leguminosae	Legume sp. 2			6		2
Malvaceae	*Abutilon benense* (Britlon)	6	6			3
Malvaceae	Malvaceae sp. 1		6			2
Malvaceae	Malvaceae sp. 2		6	6		3
Malvaceae	*Sida glabra* Mill.	25	44	69	50	47
Marantaceae	*Calathea villosa* Lindl.	25	44	63	25	39
Musaceae	*Heliconia sp.*	6	6			3
Orchidaceae	Orchid sp. 1	6				2
Orchidaceae	Orchid sp. 2	0	6	6		3
Orchidaceae	Orchid sp. 3	6				2
Phytolacaceae	*Hilleria latifolia* (Lam.)			6		2
Phytolacaceae	*Petiveria alliaceae* L.		6	13	6	6
Phytolacaceae	Phytolacaceae sp.		13			3
Phytolacaceae	*Rivinia humilis* (L.)	6		13	6	6
Piperaceae	*Piper sp.*			6	13	5
Portulacca	*Talinum trianulare* (Jacq.)		13	13		6
Rubiaceae	Rubiaceae sp. 1				6	2
Rutaceae	*Moniera trifolium* L.			6	6	3
Solanaceae	*Capsicum chacoense* Hunziker		13	6		5
Solanaceae	*Solanum apaense*		13			3
Solanaceae	*Solanum riparium* Pers.		13	25	38	19
	unknown sp. 1	6		13		5
	unknown sp. 2		13			3
	unknown sp. 3	6		6		3
liana						
Acanthaceae	*Mendoncia sp.*	44	19	50	13	31
Apocynaceae	*Forsteronia pubescens*	6	13	13		8
Apocynaceae	*Prestonia acutifolia* (Benth. ex Muell. Arg.)	6	6	13		6
Apocynaceae	Apocynaceae sp.	31	13	6	31	20
Asclepiadaceae	*Fischeria stellata* (Vell.) E. Fourn.		19	13	13	11

Appendix A. (continued)

Family	Species	Frequency (%)				
		GC	PR	LI	HI	All
Asclepiadaceae	*Gonolobus denticulatus* (Vohl) Steven			13	6	5
Asteraceae	*Mikania sp.*			6		2
Bignoniaceae	*Adenocalymma bracteatum* (Chamisso) DC.	6				2
Bignoniaceae	*Adenocalymma bracteolatum*	6	6	13	6	8
Bignoniaceae	*Adenocalymma purpurascens*			6		2
Bignoniaceae	*Arrabidaea brachypoda*				6	2
Bignoniaceae	*Arrabidaea fagoides*	88	94	94	56	83
Bignoniaceae	*Arrabidaea sp. 1*	13	6	6		6
Bignoniaceae	*Arrabidaea sp. 3*	50	38	38	31	39
Bignoniaceae	*Arrabidaea sp.2*				6	2
Bignoniaceae	Bignon. sp. 1	6	13	13	19	13
Bignoniaceae	Bignon. sp. 2	25	38	44	69	44
Bignoniaceae	Bignon. sp. 3	19	13	19	13	16
Bignoniaceae	Bignon. sp. 4	6	13	6	6	8
Bignoniaceae	Bignon. sp. 5			6	13	5
Bignoniaceae	Bignon. sp. 6		6	6		3
Bignoniaceae	Bignon. sp. 7		6	6	6	5
Bignoniaceae	Bignon. sp. 8			6		2
Bignoniaceae	Bignon. sp. 9	6				2
Bignoniaceae	Bignon. sp. 10				13	3
Bignoniaceae	Bignon. sp. 11				6	2
Bignoniaceae	Bignon. sp. 12		6			2
Bignoniaceae	Bignon. sp. 13		6	6		3
Bignoniaceae	*Clytostoma binatum* (Thunb.)	13	6		6	6
Bignoniaceae	*Cydista decora* (Spencer Moore) A. Gentry	88	75	56	31	63
Bignoniaceae	*Macfadyena sp.*	56	56	63	63	59
Bignoniaceae	*Macfadyena uncata*			13		3
Bignoniaceae	*Macfadyena unguis-cati* (L.) A. Gentry				6	2
Bignoniaceae	*Manaosella aff cordifolia* (A. DC.) Gentry					
Bignoniaceae	*Perianthomega vellozoii*	56	50	38	31	44
Bignoniaceae	*Pithecoctenium crucigerum* (L.) A. Gentry		6			2
Caricaceae	*Carica sp.*		6	6		3
Combretaceae	*Thiloa paraguariensis* Eichler	31	50	75	88	61
Convolvulaceae	Convolvulaceae sp. 1	13	13	13	19	14
Convolvulaceae	*Merremia sp.*		13	13		6
Cucurbitaceae	Cucurbit sp. 1	6	6	25	19	14
Cucurbitaceae	Cucurbit sp. 2	6	6	6	13	8
Cucurbitaceae	Cucurbit sp. 3			6		2
Cucurbitaceae	*Echinopepon racemosus* (Stued.)	19	19	19	13	17
Cucurbitaceae	*Fevillea sp.*	13	6	13	19	13
Cucurbitaceae	*Psiguria ternata* (Roem.) C. Jeffrey	6	6			3
Dioscoreaceae	*Dioscorea sp.1*				13	3
Dioscoreaceae	*Dioscorea sp.2*		6			2
Dioscoreaceae	*Dioscorea sp.3*	6	13	13	13	11
Euphorbiaceae	*Omphaleadiandra* L.	25	56	19	13	28
Euphorbiaceae	*Tragia volubilis* L.		13	31	6	13
Hippocrateaceae	*Hippocratea volubilis* L.	81	75	75	50	70
Leguminosae	*Coursetia hassleri* Chodat					

Appendix A. (continued)

Family	Species	Frequency (%)				
		GC	**PR**	**LI**	**HI**	**All**
Leguminosae	Legume sp. 1		6	6	6	5
Leguminosae	Legume sp. 2				6	2
Leguminosae	Legume sp. 3	25	50	13	31	30
Leguminosae	Legume sp. 4	6	13	19	13	13
Leguminosae	Legume sp. 5	13	13	13		9
Leguminosae	Legume sp. 6			6	6	3
Leguminosae	Legume sp. 7	6		6	6	5
Leguminosae	Legume sp. 8	38	25	38	44	36
Leguminosae	*Machaerium amplum* Benth.		6	19		6
Leguminosae	*Mimosa sp.*	88	63	69	13	58
Leguminosae	*Phaseolus sp.*	6	13	13	6	9
Leguminosae	*Rhynchosia rojasii* Hassl.	13	6	13	6	9
Liliaceae	*Herreria montevidenss* Klotzsch		6	13	13	8
Malpighiaceae	*Stigmaphyllon sp.*	6			6	3
Malpigiaceae	Malpighiaceae sp. 1	50	63	44	6	41
Malpigiaceae	Malpighiaceae sp. 2		6	13		5
Malpigiaceae	Malpighiaceae sp. 3	6	6	6	6	6
Malpigiaceae	Malpighiaceae sp. 4	19	6	25	6	14
Malpigiaceae	Malpighiaceae sp. 5			6		2
Malpigiaceae	Malpighiaceae sp. 6	6	6			3
Malpigiaceae	Malpighiaceae sp. 7	25	19	19		16
Malpigiaceae	Malpighiaceae sp. 8		6			2
Menispermaceae	*Cissampelos tropaeolifolia* DC.			6		2
Passifloraceae	*Passiflora amethystina*	6	13	13	6	9
Sapindaceae	Sapindaceae sp. 1		6			2
Sapindaceae	Sapindaceae sp. 2		6		6	3
Sapindaceae	Sapindaceae sp. 3				6	2
Sapindaceae	Sapindaceae sp. 4				6	2
Sapindaceae	*Serjania hebecarpa*		13	13	13	9
Sapindaceae	*Serjania marginata*	75	75	56	31	59
Sapindaceae	*Serjania reticulata*	81	69	56	75	70
Sapindaceae	*Serjania sp.*	75	69	81	38	66
Sapindaceae	*Serjania tripleuria*		6	6		3
Sapindaceae	*Thinouia cf. paraguayensis*			6	6	3
Sapindaceae	*Thinouia herbecarpa*	44	44	44	19	38
Sapindaceae	*Thinouia sp.*		6	6		3
Sapindaceae	*Urvillea sp.*	6				2
Trigoniaceae	*Trigonia sp.*	63	63	75	69	67
Ulmaceae	*Ulmaceae sp.*		6			2
Vitaceae	*Cissus sp. 1*		6	19	19	11
Vitaceae	*Cissus sp. 2*	44	44	69	56	53
	Unknown sp. 1				6	2
	Unknown sp. 2			13		3
	Unknown sp. 3	13	6	13		8
	Unknown sp. 4	6				2
	Unknown sp. 5	13		6		5
palm						
Palmae	*Attalea phalerata* Mart. ex Spreng.			13	13	6

Appendix A. (continued)

Family	Species	GC	PR	LI	HI	All
Palmae	*Syagrus sacona* Karsten	13	6	19	13	13
shrub						
Apocynaceae	*Tabernaemontana cymosa* Jacq.			6		2
Asteraceae	*Daciphyllum brasiliensis* (Spr.)	50	31	31	19	33
Caesalpinioideae	*Bauhinia longicuspis*	6	6	6	6	6
Capparaceae	*Capparis sp.*	19	13	6	6	11
Erythroxlyaceae	*Erythroxylum sp.*	13	44	19	19	23
Flacortiaceae	*Prockia crucis* P. Browne ex L.	38	25	50	19	33
Myrtaceae	*Calyptranthes sp.*	13		13	6	8
Myrtaceae	*Eugenia ligustrina* Kiaersk	81	81	75	63	75
Myrtaceae	*Myrcieria cauliflora* (Mart.)	13	13	6	6	9
Nyctaginaceae	*Bougainvillea modesta* Heimerd.		6	6	6	5
Nyctaginaceae	*Nyctaginaceae sp. 1*		6	6		3
Rhamnaceae	*Ziziphus sp.*	25	19	38	19	25
Rubiaceae	*Rhandia sp. 1*	19	13	6	6	11
Rubiaceae	*Rhandia armata*	6	13	56	13	22
Rubiaceae	*Rhandia sp. 2*	6		6	6	5
Rubiaceae	*Simira rubescens* (Benth). Bremek ex	13	13	13	6	11
Rutaceae	*Esenbeckia almawillia* Kaastra	25	31	38	38	33
Violaceae	*Hybanthus comunis* (St. Hil.) Taub.	81	100	88	69	84
	Unknown sp 1.				6	2
	Unknown sp 2.			6		2
	Unknown sp 3.	13	13	13	13	13
	Unknown sp 4.	13		13		6
	Unknown sp 5.	31	56	50	19	39
	Unknown sp 6.	6				2
	Unknown sp 7.			6		2
commercial tree species						
Anacardiaceae	*Astronium urundueva* (Allemao) Engl.	13	38	56	94	50
Anacardiaceae	*Schinopsis brasiliensis* Engl.			19	25	11
Apocynaceae	*Aspidosperma cylindrocarpon* Muell.	13	13		13	9
Apocynaceae	*Aspidosperma pyrifolium* Mart.		13	6	13	8
Apocynaceae	*Aspidosperma rigidum* Rusby	81	75	69	44	67
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC.)	13	13	38	44	27
Boraginaceae	*Cordia sp.*		6	6		3
Boraginaceae	*Cordia sp.*	19	13	44	31	27
Caesalpinioideae	*Caesalpinia floribunda* Tul.	63	50	56	50	55
Caesalpinioideae	*Copaifera chodatiana* Hassler	75	69	69	56	67
Meliaceae	*Cedrela fissilis* Vell.		13	6	6	6
Mimosoideae	*Anadenanthera colubrina* (Vell. Conc.)	100	100	100	94	98
Mimosoideae	*Pithecellobium sp.*	25	38	25	19	27
Papilionoideae	*Amburana cearensis* (Allemao)		6			2
Papilionoideae	*Centrolobium microchaete* (C. Marius ex Benth)	38	56	63	69	56
Papilionoideae	*Machaerium scleroxylon* Tul.	0	19	6	19	11
Papilionoideae	*Platymiscium ulei* Harms	19	6	31	6	16
Rubiaceae	*Calycophyllum multiflorium* Griseb.	6			6	5
Ulmaceae	*Phyllostylon rhamnoides* (Poisson)			6	6	3
Anacardiaceae	*Spondias mombin* L.	13	13	31	25	20

Appendix A. (continued)

Family	Species	Frequency (%)				
		GC	PR	LI	HI	All
non-commercial tree species						
Annonaceae	*Annona cf. jahnii* Saff.	6	19	19	6	13
Bignoniaceae	*Zeyheria tuberculosa* (Vell.)		6			2
Bombacaceae	*Ceiba samauma* (Mart.)					
Bombacaceae	*Chorisia speciosa* St. Hilaire	31	31	25	13	25
Bombacaceae	*Eriotheca roseorum* (Cuatrec.)	6	19	25	6	14
Bombacaceae	*Psuedobombax marginatum* (St. Hilaire)					
Caesalpiniodeae	*Bauninia angulata* L.			6		2
Caesalpiniodeae	*Poeppigia procera* C.	94	100	100	69	91
Capparaceae	*Capparis prisca* J.F. Macbr.	13	25	13		13
Caricaceae	*Carica sp.*	6	6	6		5
Cochlospermaceae	*Cochlospermum vitifolium* (Willd.)		6	6	6	5
Combretaceae	*Combretum leprosum* (Mart.)	13	13		13	9
Flacortiaceae	*Casaeria aculeata* Jacq.	13	44	19	13	22
Flacortiaceae	*Casaeria arborea* (Rich.)	56	63	63	38	55
Flacortiaceae	*Casaeria gossypiosperma* Briq.	94	88	88	81	88
Flacortiaceae	*Prokia crucis* P. Browne ex L.					
Humiriaceae	*Sacoglottis mattogrossensis* Malme.	6			6	3
Lecithidaceae	*Cariniana estrellensis* (Raddi) Kuntze	13	6	13	6	9
Lecithidaceae	*Cariniana sp.*	6				2
Meliaceae	*Trichilia elegans* A. Juss.	63	69	81	13	56
Mimosoideae	*Acacia loretensis* J.F. Macbr.	31	38	50	31	38
Mimosoideae	*Acacia polyphylla* DC.	38	63	56	38	48
Mimosoideae	*Enterolobium contortisiliquum* (Vell.Conc.)l	19	19	13		13
Moraceae	*Cecropia concolor* Willd.	6	13	31	38	22
Nyctaginaceae	*Neea hermaphrodita* S. Moore Uel	94	100	94	63	88
Nyctaginaceae	*Nyctaginaceae sp.*			13		3
Papilionoideae	*Platypodium elegans*	63	75	63	50	63
Phytolaccaceae	*Gallesia integrefolia* (Sprengel)	19	19	13	25	19
Rubiaceae	*Simira rubescens* (Benth). Bremek ex Steryerm	81	63	75	44	66
Rutaceae	*Galipea trifoliata* Aublet.	44	69	88	50	63
Rutaceae	*Zanthoxylum sp.*	44	56	50	13	41
Sapindaceae	*Allophyllus pauciflorus* Radlk.	63	69	50	19	50
Sapindaceae	*Talesia esculenta* (St. Hil.)	13	6	13	13	11
Sapotaceae	*Chrysophyllum gonocarpum* (Martius & Eichler)	6	6	6		5
Tiliaceae	*Heliocarpus americanus* L.		6	13	6	6
Tiliaceae	*Luehea paniculata* Martius		6	6	13	6
Ulmaceae	*Celtis iguanaea* (Jacq.)	25	25	19	6	19
Ulmaceae	*Trema micrantha* (L.)		44	44	25	28
Ulmaceae	*Ulmaceae sp.*	13	6	6	6	8
Urticaceae	*Urera baccifera* (L.)	38	56	38	19	38
Verbenaceae	*Lippea sp.*			6		2
	Unknown sp. 1			6		2
	Unknown sp. 2	6		6		3

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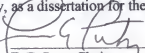
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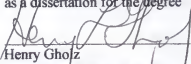
BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Botany

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